ONTOGENY, HYPOSTOME ATTACHMENT AND TRILOBITE CLASSIFICATION

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ABSTRACT. The high level classification of trilobites has proved particularly difficult. This paper discusses the classification of those trilobites which have been placed in the Order Ptychopariida, together with other relevant groups, including Agnostida. Although often considered 'generalized', the ptychoparioids have a distinctive derived character: the hypostome is not exoskeletally connected to the cephalic doublure (natant hypostomal condition). The polarity of the natant hypostome as a derived character is supported both by known ontogenies, and by comparison with other trilobites, and is unusual in primitive arthropods as a whole. The wide distribution within the Trilobita of the natant hypostomal condition is established. The primitive state, found in redlichiids, is conterminant, in which the hypostome is attached to the cephalic doublure and closely corresponds ventrally with the frontal glabellar lobe. Several trilobite groups which primitively had natant hypostomal condition became secondarily conterminant, e.g. among Asaphida and Proetida. All trilobites having natant hypostomal condition, together with those which were primitively natant and only secondarily conterminant or impendent, are believed to constitute a new monophyletic group termed the Subclass Libristoma. This group includes the majority of the trilobites. A number of major monophyletic groups within the Libristoma are recognized, and one or more autapomorphy for each group is described. The Ptychopariida can be reduced in scope to a paraphyletic group of primitive libristomates which cannot yet be assigned to a clade. The other major groups of Libristoma include: Asaphida, Proetida, Olenina, Harpina. There is slim evidence that the Phacopida also had libristomate ancestry. Some groups included in Ptychopariida in the 1959 *Treatise* can now be assigned to different higher taxa. Illaenacea (= Scutelluina) and Leiostegiacea probably belong within a large corynexochoid clade; Damesellacea are regarded as the primitive sister group of Odontopleurida. Agnostida are not libristomates, but they *are* trilobites; they are more advanced than olenellids, and comprise the sister taxon of Redlichiida + all other trilobites. An important autapomorphy defining Agnostida is the loss of calcification of an olenelloid-like rostral plate.

Natant hypostomes are conservative in morphology, and it is often difficult to assign the hypostome among natant families. Specialized hypostomes are associated with the conterminant or impendent hypostomal condition. The natant condition is lost polyphyletically, and there is some evidence that secondarily conterminant trilobites arose when primarily conterminant groups became extinct. The relationships of subgroups within the Libristoma, and the relationships of other major conterminant taxa (corynexochoids, Odontopleurida, Lichida, Phacopida) to one another and to the Libristoma remain to be explored before the taxonomic status of major groups can be decided. The Redlichiida is probably another paraphyletic group having the same relationship to all higher trilobites as does the Ptychopariida within the Libristoma.

TRILOBITES are one of the most morphologically diverse invertebrate groups with a good fossil record. Their long stratigraphical history and abundance has meant that students of the group have specialized in faunas of a particular age, or upon particular groups. It is possible to spend a productive working life studying one or two families through one or two systems, and no single worker has a detailed knowledge of the whole Class. Most specialists are concerned with classification and relationships of trilobites at subfamily, genus or species level, for which there is now an overwhelming literature. There is no uniformity of taxonomic usage throughout the group, and it is probably true that taxonomic practice tends to change, with the specialists, at system boundaries. Cambrian workers tend to be much more influenced by palaeogeography and stratigraphy than are Ordovician specialists; Devonian and Carboniferous workers tend to employ more taxonomic categories (subgenera and subspecies) than do workers lower in the column. Generally these disparities in approach cause little difficulty. However, a more important

consequence of specialization concerns classification at the taxonomic level above the family, and the relationships *between* families. Changeover between families often coincides with stratigraphical boundaries, and falls between the provinces of different specialists. The latter may take the higher categories as 'given' and concentrate instead upon the kind of within-group evolution that can be revealed by detailed stratigraphic studies. The problem is compounded by the fact that families often appear to be good, clear categories, with distinctive autapomorphies characterizing them, but the synapomorphies which can relate one family to another are far less clear. Nor have stratigraphical 'transformation series' of species connecting one higher taxonomic category with another been discovered in many cases – the families appear, as it were, ready made. Many of these natural groups were recognized already by Salter (1864, p. 2). No trilobite taxon is more intractable than the Order Ptychopariida with regard to the groups that should, or should not be included within it. Nor is it clear from the literature whether the Ptychopariida is a natural group. This paper is an attempt to approach some of these problems by discussing characters which are of service in characterizing ptychoparioid trilobites. In this endeavour I am acutely aware of the limits of my own detailed knowledge, particularly of Cambrian trilobites. But new insights into high-level classification are needed before the publication of the revision of the volume on trilobites of the *Treatise on invertebrate paleontology*.

HIGH LEVEL TRILOBITE CLASSIFICATION

The few trilobite workers who have attempted to discuss higher level trilobite classification, for example, Stubblefield (1936), Henningsmoen (1951), Harrington (*in* Moore 1959), Bergström (1973) and Fortey and Owens (1975), have stressed the need for a natural classification, by which is meant a classification that reflects phylogeny. Even so, it is apparent that higher level taxa claimed 'natural' by one worker may be disputed by another – see, for example, Bergström's (1977) discussion of Fortey and Owens' (1975) Order Proetida, and Fortey and Owens' (1979) reply. In dispute in such discussions is the meaning of particular characters: the claimed synapomorphies of one authority are disputed as homoplasies by another. Trilobites are not simple subjects for phylogenetic analysis. Cladistic analyses of character distributions offer a new approach to the problems of classification. A pioneering attempt in this direction was made by Eldredge (1977). But the cladogram he produced was based on few characters, was replete with unresolved polychotomies, and many of the groups indicated would now be in dispute. Eldredge admitted that his analysis was not satisfactory, referring to 'the chaotic and rudimentary state of our understanding of trilobite relationships' (p. 326). A very detailed account of one group, the Suborder Asaphina, which included a cladistic analysis based on a large matrix of characters, was published by Fortey and Chatterton (1988). This analysis depended on the recognition of at least one character (the ventral median suture) which served to define the whole asaphine group. Although reasons were advanced why this character was likely to be a good synapomorphy there may be workers who disagree (i.e. who claim that the median suture was polyphyletically derived). Higher Asaphina also have a distinctive kind of protaspis, and this, too, was regarded as important in recognizing the relationships of some very disparate adults. The foundation of Fortey and Chatterton's analysis was the recognition of at least one apomorphic character uniting the Asaphina.

Cladistic classifications also attempt to resolve taxonomic units into monophyletic groups (Wiley 1981). In this respect they may part company with more traditional approaches used by trilobite taxonomists in which the status of a higher taxonomic unit may be determined by some assessment of its morphological difference compared with other trilobites, rather than its common ancestry. The formal recognition of paraphyletic groups (that is, groups descended from a common ancestor, but not including all its descendants) is also common practice in existing classifications. The writer regards the definition of groups by common ancestry as a desirable goal in producing a classification which is truly 'natural'. This is not the place to develop the theoretical basis for this approach, but I broadly follow the reasoning set out previously (Fortey and Chatterton 1988) and by such authors as Jefferies (1986). However, for reasons which will become clear below, it is not always possible,

even if it is desirable, to eliminate paraphyletic taxa completely from groups with a good fossil record.

When Fortey and Chatterton (1988) treated the Asaphina, they left aside the question of the relationships of that suborder within the more inclusive Order Ptychopariida. In the *Treatise* (Moore 1959) the Ptychopariida occupies well over half the systematic section – as conceived there it is a vast assemblage of trilobites. Bergström (1973) reduced its scope, largely by elevating previous subgroups of Ptychopariida into separate orders. Of the relationships between these orders there was little discussion. Moreover, even the constituent families of Asaphina *sensu* Fortey and Chatterton (1988) were distributed among three different orders and several different suborders in Bergström's tabular classification. Nor were the characters on which the classification was based discussed in a way which is helpful for a phylogenetic classification. For these reasons a more inclusive view of Ptychopariida is the one adopted here.

The purpose of this paper is to investigate the problems in a phylogenetic definition of 'ptychoparioid' trilobites: do they constitute a monophyletic group, and if so which higher taxa may be eligible for inclusion within it? I employ the informal term 'ptychoparioid' for all the trilobites that have been considered in this context. My original intention was to tackle the problem using a computer-based cladistic analysis of probable constituent taxa, based on as many characters as possible. However, the characters that appear to be important as potential synapomorphies have either not been recognized, or not discussed in a phylogenetic context, and it is necessary to make a start by examining these characters. It is the characters which define the scope of the problem by indicating which taxa should be included in any more detailed review in the future. Although this paper concerns trilobites which have been regarded, or might prove to be Ptychopariida, it is hardly possible to avoid mentioning some of the other trilobite orders (Redlichiida, Phacopida, Corynexochida, etc.). There are problems in these groups also, but to keep the discussion within sensible bounds the discussion of such problems is briefer than it should be.

A sceptic might contend that, given the difficulties in producing a satisfactory high level trilobite classification, it might be better to adopt the 1959 *Treatise* classification (Harrington *in* Moore 1959) as a convention and forego attempts to produce a phylogenetic classification, or, like Zhang and Jell (1987), abandon all categories above family. One could at least 'pigeon hole' trilobites in this case. Such a view would quickly become self-defeating because there would be no criteria to decide the status (family? genus? superfamily?) of the various groups, and would result in a proliferation of names as more trilobites with intermediate combinations of characters were discovered. Also, broader palaeobiological theories which may be of interest to the non-specialist require a taxonomic base of 'natural' units. To cite one example, extinction patterns are a current concern, but if the 'extinction' is merely one of the disappearance of an arbitrary unit at a boundary between separate specialists it becomes meaningless (a 'taxonomic pseudoextinction' in the usage of Briggs *et al.* 1988). Conversely, it is of some interest that the extinction event at the Ordovician-Silurian boundary affects the suborder Asaphina more than any other group – a fact that was not known until the Asaphina were phylogenetically defined. I firmly believe that the recognition of natural groups is a priority in trilobite classification, even if the process is likely to prove contentious.

HYPOSTOME ATTACHMENT CONDITIONS

Fortey and Chatterton (1988, text-fig. 5) briefly introduced three terms to describe the relationship of the hypostome to the cephalic doublure on the venter, and the glabella on the dorsal surface (text-fig. 1). This character is of importance to the arguments in this paper. Whittington (1988*a*, *b*) has provided timely reviews of hypostomal attachment in the trilobites. He claimed that the anterior wings of the hypostome correspond with and were connected to the anterior pits in the glabellar axial furrows (or, if the pits are not clearly developed, to the appropriate point in the axial furrows); these structures are homologous in all trilobites. There are some differences in terminology between Whittington (1988*a*, *b*) and Fortey and Chatterton (1988) but only minor discrepancies in
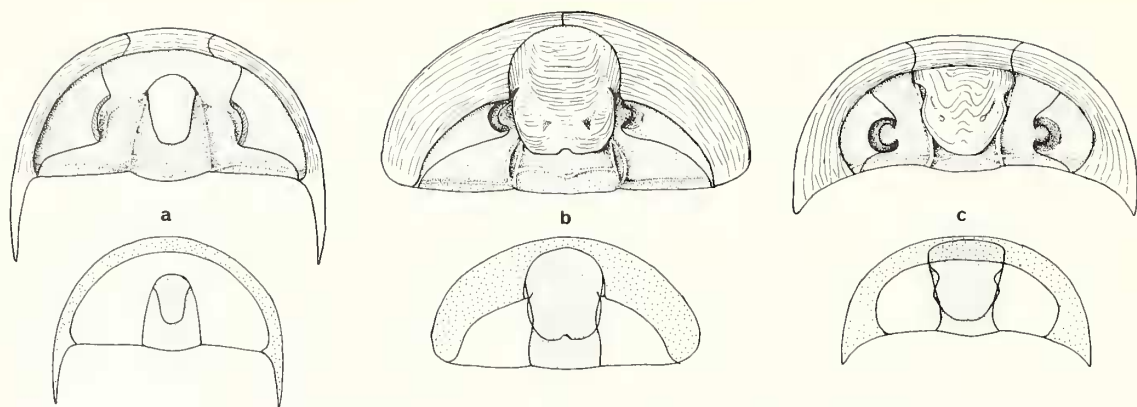
TEXT-FIG. 1. The three conditions of hypostome attachment illustrated by cephalic shields viewed from the underside. The explanatory cartoons below show cephalic doublure as coarse stipple, the outline of the glabella in fine stipple, and the hypostomal outline transparent to make clear the relationship between the hypostomal anterior margin and the preglabellar furrow. *a*, natant hypostomal condition, with 'detached' hypostome, illustrated by *Elrathia kingi*, Middle Cambrian, × 5; *b*, conterminant hypostomal condition, hypostome attached and closely correspondent with glabella outline, illustrated by *Gog catillus*, early Ordovician (after Fortey 1975), × 1; *c*, impendent hypostomal condition, with no close relationship between anterior margin of glabella and that of the hypostome (see also text-fig. 5a–c), *Raymondaspis reticulata*, mid Ordovician (after Whittington 1965), × 3.

interpretation. However, a greater emphasis is placed here on the relationships of the hypostome to other dorsal structures.

Natant hypostomal condition

This term (text-fig. 1a) was applied by Fortey and Chatterton (1988) to those trilobites in which the hypostome was not attached to the cephalic doublure, but lay beneath the front of the glabella, separated from the doublure by a gap. Whittington (1988a) used the term 'detached' to describe the same condition. Because of this absence of firm connection it is unusual to find trilobites with natant hypostomal condition with the hypostome in place. One relies upon individuals that died on their backs, the hypostome falling down into the forward part of the glabella (Rasetti 1952a) upon the decay of the soft tissue (text-fig. 2). Despite this, hypostomes of a wide range of families are known or inferred to have had natant hypostomal condition, as listed below. The existence of the same hypostomal condition can be inferred for many more trilobites of which complete remains are unknown. This is when the genal doublure (or by extension the rostral plate) corresponded in width
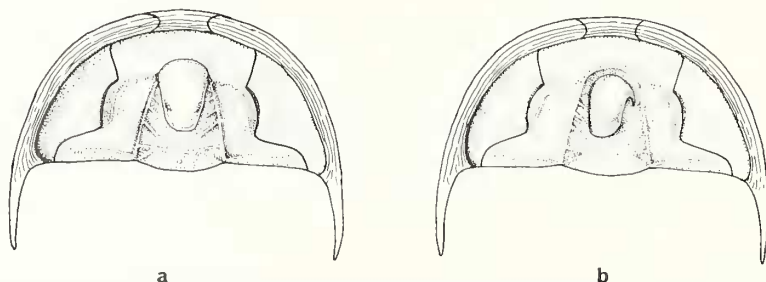
TEXT-FIG. 2. Natant hypostome in life position (*a*), and as it falls down into the glabella on death in those trilobites which died on their backs (*b*) illustrated by generalized ptychoparioid. Compare with Plate 1. Note how glabellar furrows occupy area to each side of the hypostome.

with the marginal rim (Pl. 1, fig. 2). If the marginal rim was separated from the front of the glabella by a preglabellar field, and given that the hypostome lay beneath the frontal part of the glabella (in the position consistent with the anterior wing/anterior pit correspondance), then the hypostomal condition was natant.

Those hypostomes which were not natant were rigidly attached to the cephalic doublure (Whittington 1988a, b). It is more difficult to assess the degree to which the natant hypostome was fixed in place by the anterior hypostomal wings. The fact that the hypostomes in life position are so readily displaced implies that the connection was not likely to have been particularly rigid. Also I have seen numerous examples of entire cephalic shields which should retain a natant hypostome, but of which there is now no trace (Pl. 1, fig. 2), implying that it was easily separated. Dr R. M. Owens informs me (pers. comm. 1987) that of the many proetide exoskeletons he has studied with natant hypostomal condition when the hypostome is found at all it is invariably slumped to one side in the forward part of the glabella, in the manner of text-fig. 2b, implying that its support was not rigid (a similar conclusion was reached by Whittington and Campbell 1967). For these reasons it is likely that the connection between anterior wings and anterior fossulae was ligamental, and that, in life, there was probably a degree of freedom for movement of the hypostome. For example, up and down movement of the adoral margin might have been possible by means of muscles attached to the middle furrows on the hypostomal middle body, using the ligamental attachment of the anterior wings as 'rockers'.

Natant (swimming) is an appropriate term to describe this hypostomal condition, even though the labral plate was probably tethered or anchored in at least some cases rather than truly free-lying and supported only by the ventral membrane. But some ptychoparioid hypostomes have such reduced anterior wings (e.g. *Bienvillia tetragonalis broeggeri*, see Henningsmoen 1957, pl. 11, fig. 7) that it is possible to be sceptical whether they were attached at all. The term natant is preferred to Whittington's 'detached' for two reasons: (a) 'detached' has a vernacular use which can apply to fortuitously separated hypostomes with other kinds of attachment modes; (b) if the natant hypostome is homologous in various trilobites, and is an unusual character in arthropods as a whole (below) then it requires a diagnostic epithet to describe it. Note that there is no direct connection between a trilobite having natant hypostomal condition and the configuration of the ventral sutures, so that natant hypostomes can be found with rostral plate (Ptychopariacea), median suture (e.g. Pterocephaliidae) or fused cheeks (most Olenidae).

Orientation. The connection between hypostomal anterior wings and anterior fossulae or pits in the axial furrows (Whittington 1988a) positions the hypostome in a way which corresponds with the anterior part of the glabella on the dorsal surface. This conforms with the position in which 'in place' natant hypostomes are found (see text-fig. 2 and Pl. 1). The anterior pits are in the axial furrows in front of the eye ridges, which in ptychoparioids are directed towards the anterolateral corners of the glabella. Because the anterior outline of the hypostome curves forwards, in the life orientation this profile approximates closely to the front glabellar margin, i.e. the outline of the preglabellar furrow. *The outline of the anterior margin of the hypostome closely corresponds with that of the glabella, and lies a short distance ventrally below it.* If Whittington's view of the upward projection of the anterior wings is correct (e.g. Pl. 1, fig. 5) there are some forms in which the front margin of the hypostome cannot have been far removed from the preglabellar furrow. The close correspondence dorso-ventrally between hypostome and glabella is an important point because it is retained in all trilobites except those in which the hypostomal condition is impendent.

With the hypostome restored in this position, in the typical ptychoparioid (*Ptychoparia, Elrathia* and the like) it is probable that the distribution of the glabellar furrows is related to the position of the hypostome (text-fig. 2a). The longest, posterior 1S furrows are posterior to the hypostome; the progressively shorter three anterior pairs of furrows occupy the gap between the hypostome and the edge of the glabella.

Conterminant hypostomal condition

In the conterminant hypostomal condition (text-figs. 1b, 3) the hypostome is in the same relative position with regard to the glabella as in the natant condition, i.e. the front margin of the hypostome and that of the glabella closely correspond. However, the hypostome is suturally joined to the inner edge of the doublure, and in all the described cases (Fortey and Chatterton 1988; Whittington 1988a, b) this attachment was rigid. Even in the absence of articulated material the conterminant
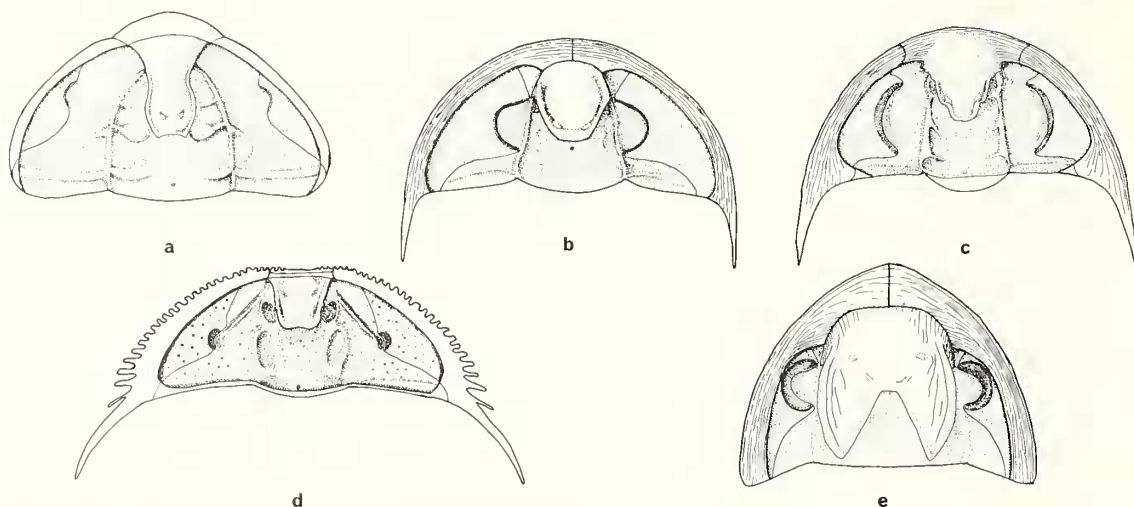
TEXT-FIG. 3. Conterminant hypostomal condition of various types, illustrated by ventral views of cephalic shields with hypostomes in place. a, the primitive calymenid *Neseuretus* (early Ordovician), in which conterminant condition is maintained by a broad anterior flange on the hypostome (mostly after Henry 1980), ×2; b, secondary conterminant hypostomal condition with backward curvature of doublure in *Proceratopyge* (Asaphida; Ceratopygidae: late Cambrian; after Jago, 1987), ×3; c, primary conterminant hypostomal condition in which rostral plate and hypostome are fused together as a single unit in *Fieldaspis* (Corynexochida: mid Cambrian; mostly after Whittington 1988a) ×3; d, primary conterminant hypostomal condition with narrow, transverse rostral plate, in the odontopleurid *Leonaspis* (Silurian; after Chatterton and Perry 1983), ×8; e, secondary conterminant hypostomal condition with hypostome recessed in doublure and occupying large part of venter, *Isotelus* (Asaphidae: middle Ordovician) ×1.

Natant hypostomal condition, including entire exoskeletons with hypostome more-or-less in life position (see text-fig. 2).

Figs. 1, 5, Olenidae: *Hypermecaspis*. 1, dorsal exoskeleton lying on its back within nodule, early Ordovician, Bolivia, USNM 380856, ×1·5. 5, hypostome from lateral view to show upward-directed anterior wings, early Ordovician, Spitsbergen, Sedgwick Museum (SM) A84079 (see also Fortey 1974, pl. 14, fig. 10), ×4.

Figs. 2, 8. Asaphiscidae: *Blainia*, two exoskeletons from same block, mid Cambrian, Alabama, USNM 62801, one showing narrow (sag.) rostral plate but lacking hypostome, the other showing hypostome in usual position in natant forms, ×4.

Fig. 3, Cedariinae: *Cedaria*, showing rostral plate and position of hypostome, U. Cambrian, Utah, USNM 300, ×4.

Fig. 4, late olenid hypostome, *Balnibarbi*, early Ordovician, Spitsbergen, SM A84021, ×5.

Fig. 6, Alokistocaridae: *Elrathia*, mid Cambrian, Utah, preserved dorsal side up but clearly showing rostral plate and position of hypostome, BM (NH) It 1734, ×2.

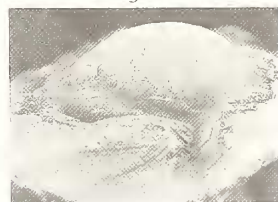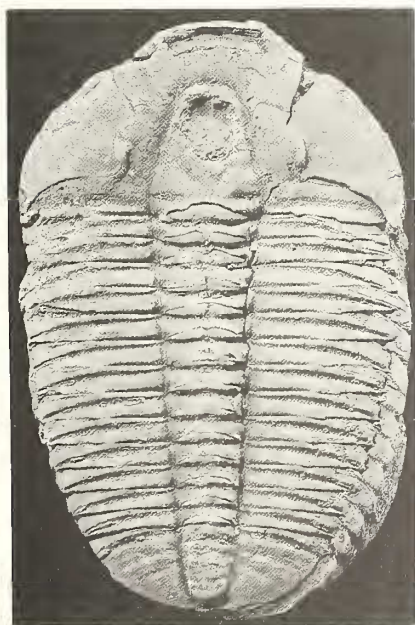Fig. 7, Proetidae; *Proetus*, Silurian, Wenlock, SM A28263 (Owens 1973, pl. 3, fig. 9), ×5.

PLATE 1

FORTEY, natant hypostomes

hypostomal condition can be inferred if the inner margin of the doublure extends as far as the front of the glabella, but no further (text-fig. 1*b*). Conterminant hypostomal condition can be found in trilobites with rostral plate, median suture, or with the cheeks conjoined ventrally. The hypostomal suture may become obsolete in trilobites with conterminant hypostomal condition, so that the hypostome and rostral plate form a single unit, as in Corynexochida (text-fig. 3*c*) and some Paradoxididae. Conterminant hypostomal condition is found in numerous trilobite families, of which several examples were described by Whittington (1988*a*, *b*) or by Fortey and Chatterton (1988): Dalmanitidae, Asaphidae, Remopleurididae, Ceratopygidae, Cheiruridae, Calymenidae, Corynexochidae, Lichidae, Odontopleuridae, Encrinuridae.

1. *Secondary conterminant hypostomal condition*. Conterminant hypostomal condition may develop secondarily from the natant condition. This is shown by examples within accepted monophyletic groups: Anomocaridae-Asaphacea; Remopleuridacea and Proetida. This secondary development is proved from stratigraphic evidence which shows that early and primitive members of the group are natant, and that later, more derived members are conterminant; and from comparison with the respective out-groups, in which the natant condition also pertains. These examples are important because they show: (a) that the conterminant condition is certainly not primitive for some Trilobita, and (b) that the conterminant condition can be attained from the natant by two different mechanisms (text-fig. 4). There is no known case where the conterminant condition returns to the natant condition – and hence it becomes a good derived character in classification.

Anomocaridae–Asaphacea. The relationships between the families included in the Asaphacea were reviewed by Fortey and Chatterton (1988). Most Asaphacea, in which Fortey and Chatterton included Ceratopygidae as well as Asaphidae, had a conterminant hypostomal condition. The primitive sister group, which probably included the common ancestor of both families, was the paraphyletic group Anomocaridae. Anomocarids certainly included some genera, such as *Anomocarioides*, which had natant hypostomal condition, the inner margin of the cephalic doublure falling well short of the front of the glabella. In fact, Fortey and Chatterton could find no member of the Anomocaracea which was convincingly conterminant. However, some species placed within this group had relatively wide cephalic doublure, so that the 'gap' between its anteromedian margin and the front of the hypostome was reduced. In early Ceratopygidae (*Proceratopyge* spp.) it was shown that the hypostome was attached to the doublure, and this was achieved by a median widening of the doublure (Jago 1987). This widening was indicated on the dorsal surface by adaxial backward curvature of the paradoublural line(s). In Asaphidae the doublure is wide both beneath free cheeks, and under the (usually wide) preglabellar area, before terminating on a line coincident with the preglabellar furrow (text-fig. 1*b*). The relatively great width of the cephalic doublure possible in this group suggests that the preglabellar field was 'lost' by backward extension of the doublure beyond the marginal rim at which it terminated in the ptychoparioids. In some conterminant asaphids doublure and frontal area are again narrow, but stratigraphic evidence suggests that this narrowness may be secondary. In any case the anomocarid-asaphacean transition (text-fig. 4a) involves secondary docking of the hypostome with the doublure – which may become very wide in the process – and attendant loss of the natant hypostomal condition. A few advanced asaphaceans attain the impendent hypostomal condition.

Remopleuridacea and Dikelocephalacea. These two superfamilies were regarded as closely related within the Asaphina by Fortey and Chatterton (1988), and Dikelocephalacea is used in the sense of Ludvigsen and Westrop (1983) to include Ptychaspidacea of authors. Early Remopleuridacea, such as kainellids and *Elkanaspis* Ludvigsen, 1982 have a narrow marginal cephalic rim, and the doublure ventrally corresponds with the rim. Species having a wide preglabellar field are therefore likely to have had natant hypostomal condition (Fortey and Chatterton 1988, text-fig. 14). In later and more advanced Remopleuridacea, especially *Apatokephalus* and its allies, the glabella extends forwards as far as the border, and the width of the cephalic doublure medially (e.g. Ross 1951, pl.

backward extension
of doublure

CONTERMINANT

loss of preglabellar
field

NATANT

a

b
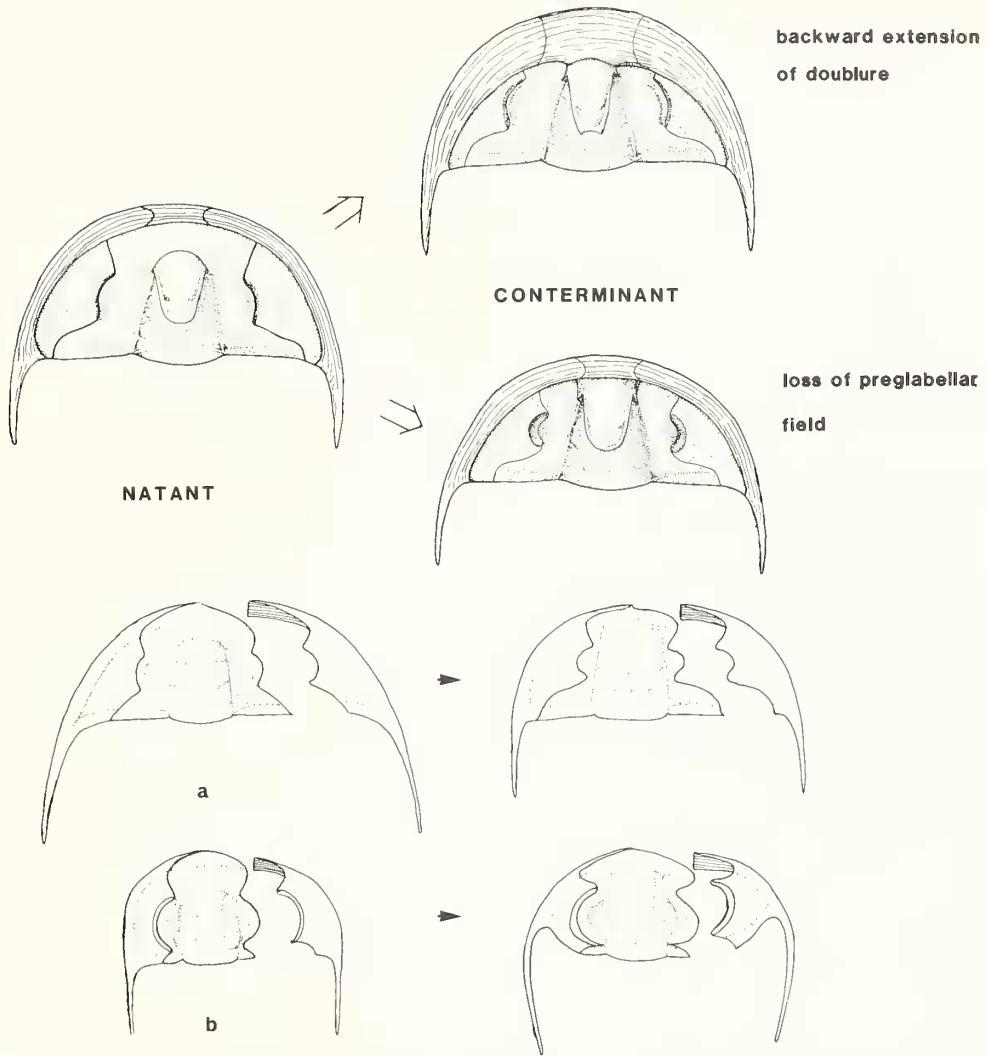
TEXT-FIG. 4. Two possible mechanisms (above) for attaining secondary conterminant hypostomal condition from natant hypostomal condition illustrated by generalized ptychoparioid of elrathiid type. Two examples (below) of secondary conterminant condition, primitive natant morphology to left and position of hypostome shown as dotted outline: *a*, anomocaracean *Litocephalus* (after Palmer 1960) (left) and primitive asaphid *Promegalaspides* (right); *b*, remopleuridaceans *Elkanaspis* (left) and *Menoparia* (right) (after Fortey and Chatterton 1988).

20, fig. 30) indicates that the hypostome had docked at this stage to become conterminant (text-fig. 4*b*). In the most advanced members of the family Remopleurididae the glabella has encroached forwards still further so that the hypostomal condition becomes impendent, and the rigid hypostomal attachment of such forms has been familiar for some time through the work of Whittington (1959). Remopleuridacea thus afford a second example of secondary conterminant condition having been attained from a natant condition. Unlike at least some of the Asaphacea, the achievement of conterminant hypostomal condition was made by elimination of the preglabellar field by forward encroachment of the glabella – the cephalic doublure remains coincident with the

cephalic rim as it is in ptychoparioids. Even though the conterminant hypostomal condition is functionally the same as it is in asaphaceans it seems possible that the means of achieving it may be different.

Less is known of ventral structures in Dikelocephalacea. Conterminant hypostomal condition certainly pertained in saukiids such as *Saukia*, and also in ptychaspids with a narrow tube-like cephalic doublure, and in dikelocephalids, such as *Dikelocephalus*, with a wide and flat doublure. Idahoiidae may prove to be the sister group of Dikelocephalacea, and idahoiid genera such as *Wilbernia* and *Idahoia* show wide borders, but which do not reach the front of the glabella; these were in all probability still natant.

Proetida. The Order Proetida Fortey and Owens, 1975 includes numerous post-Cambrian families, and was the only trilobite group to survive the Devonian. I shall return to the characters defining it below. Early Proetida, and perhaps the majority of the Order, have natant hypostomal condition. The cephalic doublure closely corresponds with the cephalic rim, the two together forming a tube-like structure in many proetides. Natant hypostomal condition is accordingly obvious for Proetacea having narrow borders and wide preglabellar fields, such as the primitive genus *Decoroproetus* (Owens 1973, pl. 7, fig. 15), and the majority of Aulacopleuridae. On more advanced genera with reduced preglabellar field, such as *Proetus* itself, it is not immediately clear whether the hypostome is or is not attached to the doublure, but specimens preserved 'on their backs' (e.g. *Proetus concinnus* (Dalman), see Owens 1973, pl. 3, fig. 9; Pl. 1, fig. 6 herein) show the hypostome in the fallen position typical of other taxa with natant hypostomal condition. The same lack of attachment of the hypostome probably persisted into the Carboniferous in such genera as *Nanuropyge*, which has a preglabellar field, and certain *Cummingella* species (e.g. Woodward 1883, pl. 1, fig. 4*a*). However, some Proetida *did* attain secondary hypostomal attachment, as shown in text-figure 5. For example, the Carboniferous genus *Paladin* (Whittington 1988*b*, text-fig. 12) has the glabella encroaching on the cephalic border, and the hypostome is attached to the doublure in the typical conterminant fashion (also text-fig. 5*d*); the same probably applied to many other Carboniferous phillipsiids. Campbell (1977; also Whittington 1988*b*) showed that the cephalic doublure on the Devonian brachymetopid genus *Cordania* was relatively wide – wider than the 'border' – and terminated precisely on a line around the front of the preglabellar furrow. If it was in its usual position co-incident with the glabellar frontal lobe it is not unreasonable to assume that the hypostome was conterminant in this case also, although there are no examples known to me of brachymetopids with hypostome *in situ*. Campbell (1977, p. 20) thought that the 'border' furrow in this case was not homologous with that in other Proetida (the contrary opinion was held, for example, by Owens and Thomas 1975), which he regarded as really coincident with the inner doublural margin. If this view is correct then loss of the natant hypostomal condition would be the result of encroachment of the glabella on the border as in *Paladin* and remopleuridids. However, if the other view is held – that the doublure has 'grown beyond' the true border – then the loss of the natant condition was the result of the doublure growing out to meet the hypostomal margin, a case like the Asaphacea described above (and text-fig. 3, top). Whatever the correct interpretation of border homology, these proetaceans evidently show the secondary acquisition of conterminant hypostomal condition by analogous mechanisms to those operating in Asaphina.

Non-proetacean Proetida include several families in Fortey and Owens' (1975) concept. Their original scenario was that these were ultimately derived from the subfamily Hystricurinae, a typically 'ptychoparioid' group with narrow cephalic rims and doublures (e.g. Ross 1951, pl. 8, figs. 7 and 8) and wide enough preglabellar fields to be likely to have had natant hypostomal condition. Early Bathyuridae (*Peltabellia*, see Ross 1951) were generally like hystricurids in these features and there is no reason to suppose that they were other than natant. However, some advanced forms with reduced preglabellar fields, such as *Bathyurus* itself, have been claimed as having rostrum and hypostome in contact (Ludvigsen 1979); Whittington (1988*b*) also considered that the hypostome was firmly braced in *Bathyurus*. Whittington (1963, pl. 11, fig. 6) figured the cephalic doublure of the bathyurelline *Punka nitida* (Billings) which is wider than in hystricurids but does not extend
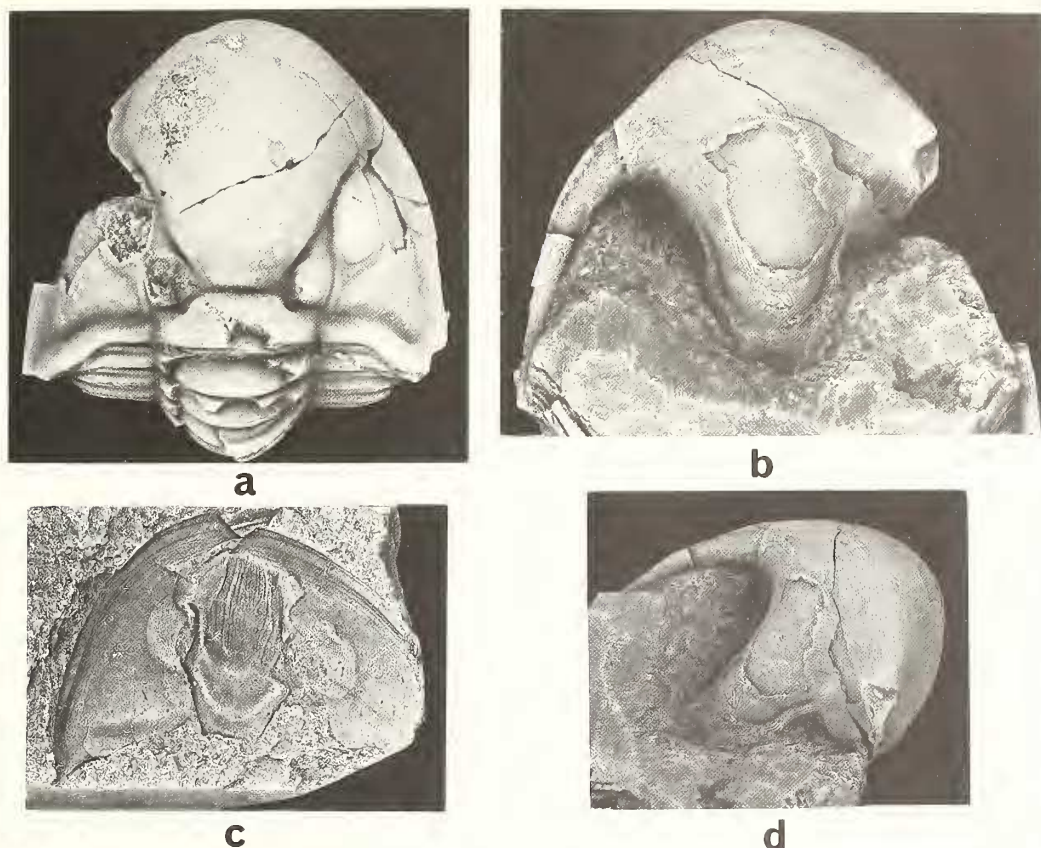
TEXT-FIG. 5. Secondarily attached hypostomes in Proetida. *a*, *b*, *d*, impendent hypostomal condition in *Griffithides acanthiceps* Woodward; Dinantian, Treak Cliff, Castleton, Derbyshire: *a*, dorsal, and *b*, ventral views, ×6; *d*, oblique ventral view, ×5. Note anterior pits in axial furrows well posterior to usual position in natant forms. National Museum of Wales (NMW) 86.25G.2332. *d*, Secondary conterminant hypostomal condition in *Archegone* (*Phillibole*) aff. *aprathensis* Richter and Richter, Dinantian, slopes of Pendle Hill, Lancashire. ×3, NMW 88.36G.10. Photographs kindly supplied by R. M. Owens.

across the preglabellar field. Ross (1953) described the silicified hypostome of another bathyurelline, *Licnocephala cavigladia* Hintze, which shows remarkably long prong-like anterior wings and a poor match between anterior profile of hypostome and posterior margin of cephalic doublure. It seems then, that in Bathyuridae secondary conterminant condition occurred only rarely, and only in the stratigraphically youngest members of the family. Nor are there any described examples of Dimeropygidae or Glaphuridae in which conterminant hypostomal condition is suspected.

To summarize, Proetida primitively have natant hypostomal condition, and some families remain so. Several other proetide families include advanced members in which the hypostome is secondarily conterminant; this happens by the loss of the preglabellar field by encroachment of the glabella on the border, or, possibly, by widening of the doublure to cover the preglabellar field. The former happens also in the Remopleuridacea; the latter in the anomocarid – asaphid – ceratopygid transition. In no case is there a reversal from conterminant back to natant.

2. *Primary conterminant hypostomal condition*. In the cases just described the conterminant hypostomal condition is derived, within accepted monophyletic groups, from the natant condition. Although these trilobites provide the theme of this paper, it is important to recognize that there are

other trilobite groups with conterminant hypostomal condition in which it is not derived from the natant condition; indeed, it is considered to be the primitive mode of hypostomal attachment for the Trilobita as a whole.

The primitive state: Redlichiida. The Redlichiida are regarded as the sister taxon of all 'higher' trilobites, which excludes only the Agnostida and olenelloids (see text-fig. 14), and includes all ptychoparioids. Redlichiids have functional dorsal ecdysial sutures and have a rostral plate bounded by connective sutures. Following Bergström (1973) and Fortey and Whittington (1989), olenelloids are regarded as primitive trilobites lacking dorsal ecdysial sutures, a view different from that of Lauterbach (1980), who regarded certain olenelloids as more closely related to chelicerates. Ax (1987) summarized Lauterbach's views in English. Here it may be stated that the greater number of derived characters favour the trilobite hypothesis of olenelloid relationships, if the characters identified as synapomorphies by Fortey and Whittington (1989) are correct. The systematic position of the Agnostida is discussed below. If the Redlichiida is correctly identified as the sister group of higher trilobites the redlichiid mode of hypostomal attachment (text-fig. 6) is the primitive one for such trilobites.

TEXT-FIG. 6. Conterminant condition as the primitive hypostomal attachment mode as exemplified in Redlichiida, the sister taxon of 'higher' trilobites. *Redlichia longtangensis* Zhang and Lin (see Zhang *et al.* 1980, text-fig. 53), late Lower Cambrian, Longtang, E. Guizhou, China, showing extension of cephalic doublure and position of hypostome, × 1·5. Nanjing Institute of Geology and Palaeontology 7057. Photograph kindly supplied by W. T. Chang (Zhang Wentang).

Lauterbach (1980) regarded the Emuellidae as the primitive sister group of redlichiids. Pocock (1970, text-fig. 4) clearly described the nature of the attachment of the hypostome in *Emuella*. It is conterminant, the anterior edge corresponding both with the front of the glabella dorsally, and the back end of the relatively narrow (tr.) rostral plate. In *Redlichia* (Öpik 1958; Zhang *et al.* 1980; Whittington 1988*a*) the hypostomal attachment is similar, that is, conterminant (also *Resserops*, see Hupé 1953, fig. 39). Öpik (1958) showed that the rostral plate and hypostome are fused together in *R. idonea* Whitehouse, whereas in *Emuella* 'the hypostomal suture is functional' (Pocock 1970, p. 528). Of numerous *Redlichia* species figured by Zhang *et al.* (1980) some (e.g. pl. 20, fig. 5) have

hypostomes without attached rostrum, as does *Sardoredlichia* (Rasetti 1972, pl. 9, fig. 19), and it seems likely that the fusion of rostrum and hypostome was an advanced, not a primitive character. Additional evidence for this can be cited in that such secondary fusion happens again, later, in some species only of *Paradoxides* (Whittington 1988*a*), and in the Corynexochida. The important point is that the primitive mode of attachment in the group Redlichiida + all other non-olenellid trilobites is conterminant. This can be referred to as *primary conterminant hypostomal condition*. This is **not** homologous with the secondary conterminant hypostomal condition, described above, in which it is derived from the natant hypostomal condition.

Certain redlichiids develop a short preglabellar field: see, for example, *Redlichia yichangensis* Zhang and Lin (*in* Zhang *et al.* 1980) and *R.* (*Pteroredlichia*) *chinensis* Walcott (Zhang *et al.* 1980, pl. 25, fig. 5). This does not mean however, that the hypostome became detached from the rostrum and natant. Zhang *et al.*'s pl. 20, fig. 9 and pl. 25, fig. 25 clearly show the hypostome in place beneath the frontal glabellar lobe, and the cephalon in the latter also shows that the posterior part of the rostral plate extends backwards (see text-figure 6) across the 'gap' between marginal rim and preglabellar furrow. Conterminant hypostomal condition is retained. Many redlichiids for which ventral structures are not known show a median plectrum in the preglabellar field (e.g. Zhang *et al.* 1980, pl. 21, fig. 7), and it is my contention that this is the dorsal expression of such a backward extension from the rostral plate. A plectrum is a median backward projection of the border, and usually distinctly defined; however, other redlichiids show a vaguer median depression in the same region, which may still represent the same ventral structure.

Incidentally, whether or not olenellids *were* trilobites, they do appear to show some comparable ventral structures to redlichiines. Some, such as *Hohnia*, were clearly conterminant, with close connection between doublure and hypostome (Whittington 1988*a*). Others, such as *Olenellus*, show narrow spine-like connections across the preglabellar field, and median plectra dorsally.

Other probable examples of primary conterminant hypostomal condition. If the conterminant hypostomal condition is primitive for the higher trilobites as a whole it is not surprising that it is retained in many families. Some of these were reviewed by Whittington (1988*a*, *b*). In some groups the conterminant condition intergrades with the impendent condition discussed in the following section. In many trilobite families the conterminant condition is constant, and retained during modifications to the border. For example, in the calymenid *Neseuretus* (text-fig. 3*a*) the cephalic border is exceptionally extended for the family and the conterminant hypostomal condition is retained by virtue of an anterior plate-like extension of the hypostomal margin which extends beneath the area between the front of the glabella and the anterior cephalic rim. There is no *a priori* reason why *Neseuretus* should not have become natant – i.e. the hypostome simply 'drifted away' from the rostrum as the border extended – but the fact that this does not happen proves the conservatism of the hypostomal attachment mode.

A list of non-redlichiid higher taxa having primary conterminant hypostomal condition includes the following, most of which I have confirmed through examination of specimens in the British Museum (Natural History) collections. This list is not hierarchically arranged, and those taxa discussed above under secondary conterminant hypostomal attachment are not included.

Order Corynexochida: Most of this group are conterminant (text-fig. 3*c*); a few advanced forms may possibly have been impendent. Loss of hypostomal suture by ankylosis may make the anterior limits of the hypostome difficult to see in some cases.

Superfamily Leiostegiacea: Apparently all are conterminant, but there are no described examples with hypostome in place. The doublure-hypostome relationship is fairly obvious in those genera, like *Leiostegium* itself (text-fig. 17*a*, p. 564), with distinct anterior pits far forwards in the axial furrows with which the anterior wings of the hypostome would have engaged. Broad-bordered genera like *Palocorona* Shergold, 1980 develop a 'false border furrow' but the course of the inner margin of the doublure is still revealed by the paradoublural line extending to the front of the glabella.

Superfamily Damesellacea: These have not been fully described from the ventral side, but examination of *Stephanocare* and *Blackwelderia* specimens in the B.M. (N.H.) shows that the cephalic doublure is closely

coincident with the cephalic border, which is narrow and ledge-like in front of the glabella, a structure very like that of the Leiostegiacea. The hypostomes of several genera are known, and assuming the correspondence of anterior wings with the anteriorly placed pits in the axial furrows, it seems likely that the Damesellacea were also conterminant.

Superfamily Cheiruracea: Many entire specimens of cheiruraceans have been described (Lane 1971; Whittington 1988*b*; Jell 1985, pl. 13, fig. 10); all Pliomeridae and Cheiruridae are conterminant, except where the frontal lobe of the glabella has expanded forwards (especially Encrinuridae; some Cheiruridae) and incorporated the border within it, and these may perhaps be better described as impendent.

Superfamily Calymenacea: Advanced calymenids are consistently conterminant, even when, as in *Neseuretus* (above), the preglabellar area is long. The extended preglabellar area in this case is 'covered' by an extension of the hypostome, but this is unusual. Homalonotids with extended (sag.) borders, and such calymenids as *Calymenesun* (Derek J. Siveter pers. comm. 1986) cover the extended area by growth of the rostral plate and the adjacent genal doublure. The hypostome remains in its usual position. So far as can be ascertained primitive calymenaceans with preglabellar field were also conterminant. For example *Prionocheilus* (= *Pharostoma*) appears to show a backward extension of the rostral plate sufficient to bridge the distance between anterior border and the front of glabella and hypostome (Whittard 1960, pl. 18, fig. 4).

Suborder Phacopina: Jaanusson (1975) discussed the morphological steps leading to the suborder Phacopina, and described *Gyrometopus* as a primitive representative. This genus had a rather narrow cephalic doublure, but the hypostome is not known and it is difficult to say whether it was or was not conterminant. The more primitive Phacopina are classified within the Dalmanitidae. Many of the stratigraphically early dalmanitids described by Henry (1980) show details of the ventral cephalic surface, including hypostomes in place (Henry 1980, pl. 28, fig. 4; pl. 29, fig. 4). These were probably conterminant. Early Pterygometopidae, such as *Calyptaulax* (e.g. Chatterton and Ludvigsen 1976, pl. 16) are apparently slightly impendent. Phacopidae are impendent, even early genera such as *Morgatia* (Henry 1980, pl. 43, fig. 6).

Order Odontopleurida: Odontopleurids (text-fig. 3d) are known from numerous silicified species; they are all conterminant (see, for example, cephalic shields of several species figured by Chatterton and Perry 1983). Both cephalic border and doublure are narrow, and the hypostome is rigidly attached (Whittington 1988*b*).

Order Lichida. Thomas and Holloway's (1988) recent review of this group shows conterminant condition to be the rule.

This brief review shows that, although the conterminant condition is primitive for the higher Trilobita, it is present, and consistently so, within a variety of higher taxa extending to the later history of the group. While it is likely that in mid-Cambrian groups this is a retained plesiomorphic character, there is at least the possibility among later groups such as the Calymenacea that it is secondarily derived from the natant condition, as in Asaphina and Proetida, and if so this would have considerable taxonomic implications. I return to this topic below.

Impendent hypostomal condition

In the impendent hypostomal condition (text-figs. 1*c*, 5*a–c*) the close relationship between the position of the hypostome and the front of the glabella which pertains in natant or conterminant hypostomal condition is lost. The term was coined by Fortey and Chatterton (1988) with reference to Cyclopygacea, but applies to many other groups. Its taxonomic importance is proved by the fact that there is no known example where impendent hypostomal condition reverts to conterminant or natant. The impendent condition results from the relative forward growth and often inflation of the glabella to engulf the cranidial border; in the process the anterior glabellar margin more nearly coincides with the cephalic margin, and the hypostomal suture occupies a relatively posterior position. The relationship between the anterior wing of the hypostome and its connection in the axial furrow is not lost. This is shown by the hypostomes of *Nileus* and *Remopleurides*, for example, in which the anterior hypostomal wings become elongated in the dorsal direction (e.g. Whittington 1965, pl. 31, figs. 2 and 3; 1988*b*, text-figs. 5 and 6). Impendent hypostomal condition can characterize higher level taxa (Cyclopygacea, Illaenina, Phacopidae), and is independent of the development of the ventral sutures, occurring with rostral plate (*Illaenus*), median suture (*Amphytrion*) or fused cheeks (*Symphysurus*, *Phacops*).

In those groups which attained secondary conterminant hypostomal attachment a number of subgroups went further to become impendent (Cyclopygacea, some Asaphinae, some phillipsiids

such as *Griffithides* and *Hentigia*, see Whittington 1988*b*). It is clear in these that there is a morphological and phylogenetic progression running natant – secondary conterminant – impendent. Impendent hypostomal condition may have been capable of developing directly from primary conterminant condition. But in, for example, Corynexochida (*Corynexochus*) having the glabella extending far forwards it is likely that the rostral plate became extremely narrow (sag.) and impendent attachment was not attained.

A detailed discussion of the impendent condition is not as important to the phylogenetics of Ptychopariida as is the conterminant condition, but it is important in the wider context of trilobite classification. In addition to those Asaphina mentioned already several large groups are typified by having impendent hypostomal condition:

Superfamily Illaenacea: as restricted to Illaenidae plus Scutelluidae, and excluding groups placed in Proetida by Fortey and Owens (1975). Even early members of this group such as *Raymondaspis* (Whittington 1965, pl. 57, fig. 9) appear to have the glabella extending well beyond the inner doublural margin.

Advanced Phacopida: The Phacopidae, Calmoniidae and Monorakidae are all impendent. The first two of these groups had their origins in the Ordovician, and presumably had sister groups within what would at present be classified as dalmanitaceans having conterminant hypostomal condition.

Late Proetida: A number of stratigraphically late genera of Proetida have glabellas that expand forwards to the cephalic margin – much in the manner of Nileidae in the Asaphina. Examples would include the Permian genus *Paraphillipsia* (see Owens 1983), and *Griffithides* (text-fig. 5*a*–*c*). Because such forms had cephalic doublures of normal width they would have had impendent hypostomal condition also. They must have been derived from one of the secondarily conterminant proetides.

One example will suffice to show that the discrimination of the different modes of hypostomal attachment can be of immediate taxonomic use (text-fig. 7). Bornemann (1883) described the trilobite *Illaenus meneghinii* from Sardinia, which subsequently became the type species of
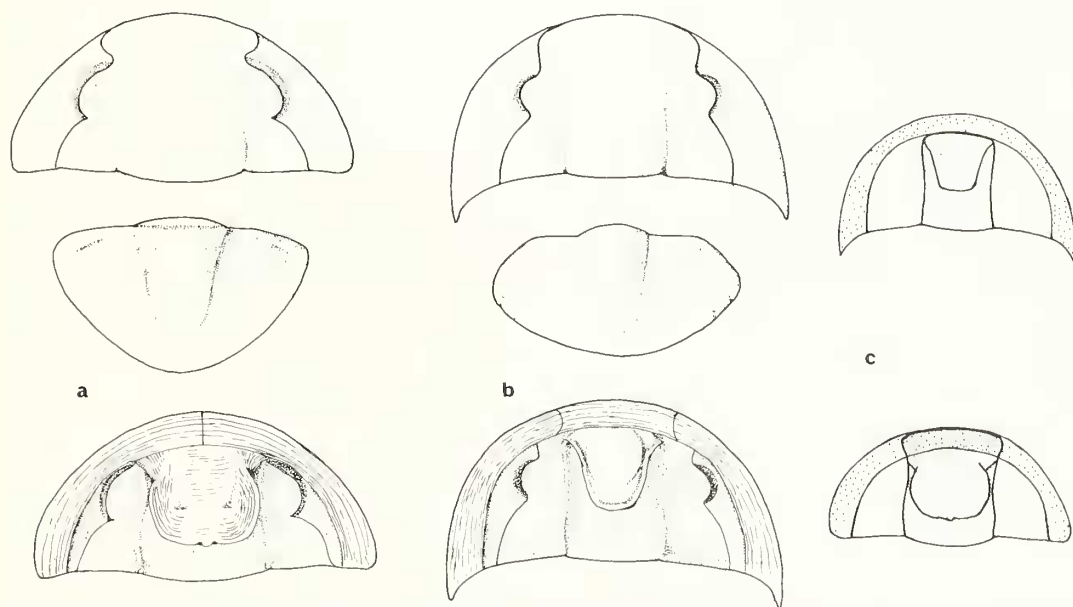
TEXT-FIG. 7. Hypostomal attachment condition as a key to revealing homoeomorphy. *a* and *b*, dorsal cephalic and pygidial morphology of the early Ordovician genus *Platypeltoides*, and the early Cambrian genus *Giordanella* (after Rasetti 1972) showing general similarity, *c*. × 3. Below, inferred ventral views of the same. *c*, cartoons illustrating hypostomal attachment mode using same conventions as in text-figure 1, *Giordanella* above, probably conterminant, *Platypeltoides* below, impendent.

Giordanella. Because of the general resemblance of *Giordanella* to early Ordovician Nileidae, the beds yielding it came to be regarded as transitional between Cambrian and Ordovician. Later it became apparent that the horizon was, in fact, Lower Cambrian, and the time gap between this horizon and the early Ordovician was so considerable that Nicosia and Rasetti (1971) rejected nileid affities in favour of *incertae familiae*. Rasetti (1972, p. 44) went further in using *Giordanella* as a good example of how homoeomorphy confuses and, by implication, as part of his argument on how misleading the morphology of Cambrian trilobites can be 'without taking into consideration the age and geographic province'. In the present context, it is clear that, effaced dorsally though it is, the cranidium of *Giordanella* can show the anterior outline of the glabella (e.g. Rasetti 1972, pl. 10, figs. 3, 9) well inside the cranidial margin. The Family Nileidae, and the superfamily Cyclopygacea to which it belongs, are characterized as having impendent hypostomal condition, and as a consequence the glabella dorsally extends to the cephalic margin. There is thus an easy way to show that *Giordanella* and, for example, the nileid *Platypeltoides*, a genus it generally resembles dorsally (text-fig. 7), are not related. If one adds to this the fact that *Giordanella* has a wide rostral plate (Rasetti 1972, pl. 10, fig. 22) whereas the Nileidae either have a median suture or fused cheeks, then the likelihood of a close taxonomic relationship between nileids and *Giordanella* becomes remote. *Giordanella* probably had primary conterminant hypostomal condition, if we are to judge from the width of the doublure and the indication of a paradoubural line running to the front of the glabella. This suggests a comparison with the family Ellipsocephalidae, which is widespread and familiar in the Lower Cambrian. *Giordanella* would then become just another example of a relatively macropygous and effaced trilobite, which is known to be one of the most iterative (and therefore of least taxonomic moment) trends in trilobite evolution (Lane and Thomas 1983). One might perhaps turn Rasetti's argument on its head and use this example to demonstrate that it is necessary to look at characters critically first before jumping to stratigraphical conclusions based on general resemblance.

NATANT HYPOSTOMAL CONDITION AS A SHARED DERIVED CHARACTER

It was concluded above that the primitive hypostomal attachment mode is conterminant. If so, the natant condition is a derived character and hence a synapomorphy of potential use in defining a monophyletic group. Öpik (1963, p. 77) has already stated that the natant hypostomal condition is of importance in higher level trilobite classification. There are a few criteria which can be used to establish the polarity of a character shift (Schoch 1986, pp. 134–142) – in this case, that the natant condition is a derived character. The comparison with *Redlichia* described above exemplifies the criterion of comparison with the out-group. There is also the criterion of ontogeny: during morphogenesis the developmental sequence should parallel the inferred polarity (conterminant to natant in this case). The stratigraphic criterion suggests that the primitive condition will also be stratigraphically earlier. Whittington (1988*a*) has shown that the natant condition (his 'detached') pertained in the type species of *Ptychoparia* – and so it will be, by definition, a ptychoparioid character. In order to establish how unusual the natant hypostome is as a derived character it is also worth looking at a wider range of arthropod out groups. If unusual, then it is reasonable to attribute to it some 'weight' in classification.

How unusual a character is the natant hypostome?

The relationship of the trilobites to the other Arthropoda is not resolved (Cisne 1974; Hessler and Newman 1975; Lauterbach 1980; Schram 1986). Most authors would agree that they are part of a clade that includes both crustaceans and arachnates. A preliminary cladistic analysis by Briggs and Fortey (1989) indicated that the trilobites were advanced relative to crustacean groups. Antennae and biramous trunk limbs were primitive attributes of the crustacean/arachnate clade. There is no occasion here to discuss the different theories of trilobite relationships but it is worth considering the Crustacea as an out-group for hypostomal attachment. The homologue of the hypostome may be the labrum (labral plate if sclerotized), and, if so, 'labral plate' is probably the

correct morphological term for hypostome, although it has been used by few authors (e.g. Jaanusson 1975). In crustaceans the labrum *is* attached to and continuous with the dorsal cuticle. There is no consensus about what constitutes the most primitive living crustacean, but the attached labrum applies whether this is taken as a remipede (Schram 1986), or a cephalocarid (Sanders 1963) or a notostracan (text-fig. 8). The same attachment is observed even in highly specialized crustacean groups such as the copepods (Boxshall 1982, text-fig. 46), and is apparently invariable. In the nauplius larva, which is generally regarded as primitively present in Crustacea, the labrum is prominent (text-fig. 8), and a comparison may be drawn with the prominent hypostome of trilobite protaspides.

Hence, if the attached labral plate is so widespread among these crustacean groups, then the detached, natant condition becomes the more unusual as an advanced, apomorphic character.

a   b   c
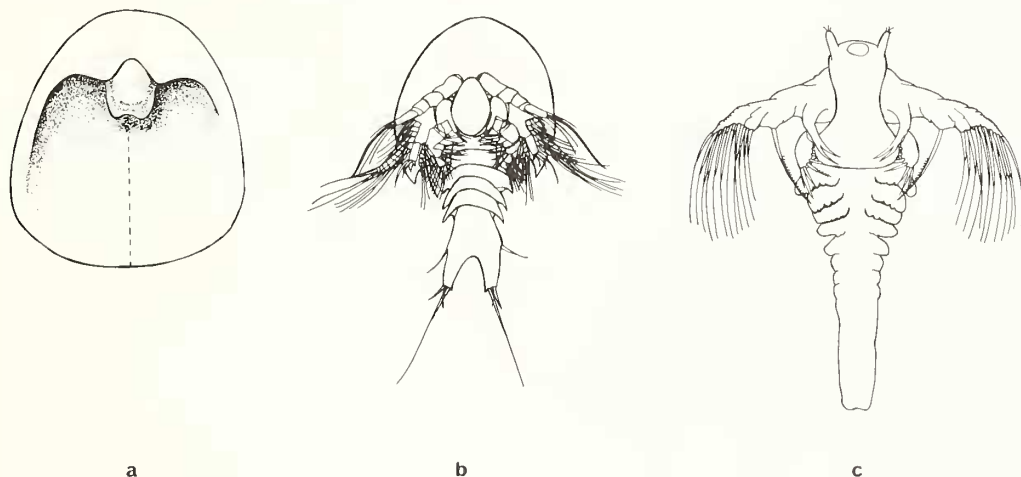
TEXT-FIG. 8. Labral plate attached to carapace in primitive crustaceans and their early growth stages. *a*, carapace of notostracan *Triops*; *b*, immature cephalocarid *Hutchinsoniella* (after Sanders 1963); *c*, anostracan *Artemia* nauplius (after Sanders 1963).

*Ontogenetic evidence for character polarity*

Trilobites are unusual among fossil groups in having the exoskeletal ontogeny nearly completely preserved, and described from numerous taxa. It is feasible to see how the natant hypostomal condition arises during ontogeny. The earliest larval stage is the protaspis. Protaspides of some species are known with the hypostome in place, but many more are known from the dorsal shield minus cheeks. The hypostome is invariably prominent in complete protaspides, occupying a relatively large area of the venter by comparison with meraspides or adults. In all protaspides from which the hypostome is described it was attached to the doublure (see, for example, Whittington *in* Moore 1959; Fortey and Chatterton 1988, fig. 10; text-fig. 10*a–g* herein). The protaspis did not have natant hypostomal condition. Even in those protaspides for which the hypostome is not known it can be inferred that it was attached. This is because the anterior pits are often prominent near the anterior margin of the glabella, and the glabella extends far forwards (see text-fig. 10*h–m*), so that the correspondence of anterior pits with hypostomal attachment means that the hypostome had to be adjacent to the cephalic doublure in the usual position. The prominence of the anterior pits in many protaspides is presumably a reflection of the large relative size of the hypostome. Such prominent pits are even visible on smoothed out, planktic, asaphoid protaspides such as those of asaphids (Tripp and Evitt 1986), nileids (Fortey and Chatterton 1988) and remopleuridids (Whittington 1959), where they may afford the only evidence of the extent of the cephalic axis (text-fig. 10*m*). The only possible exceptions are discussed below.
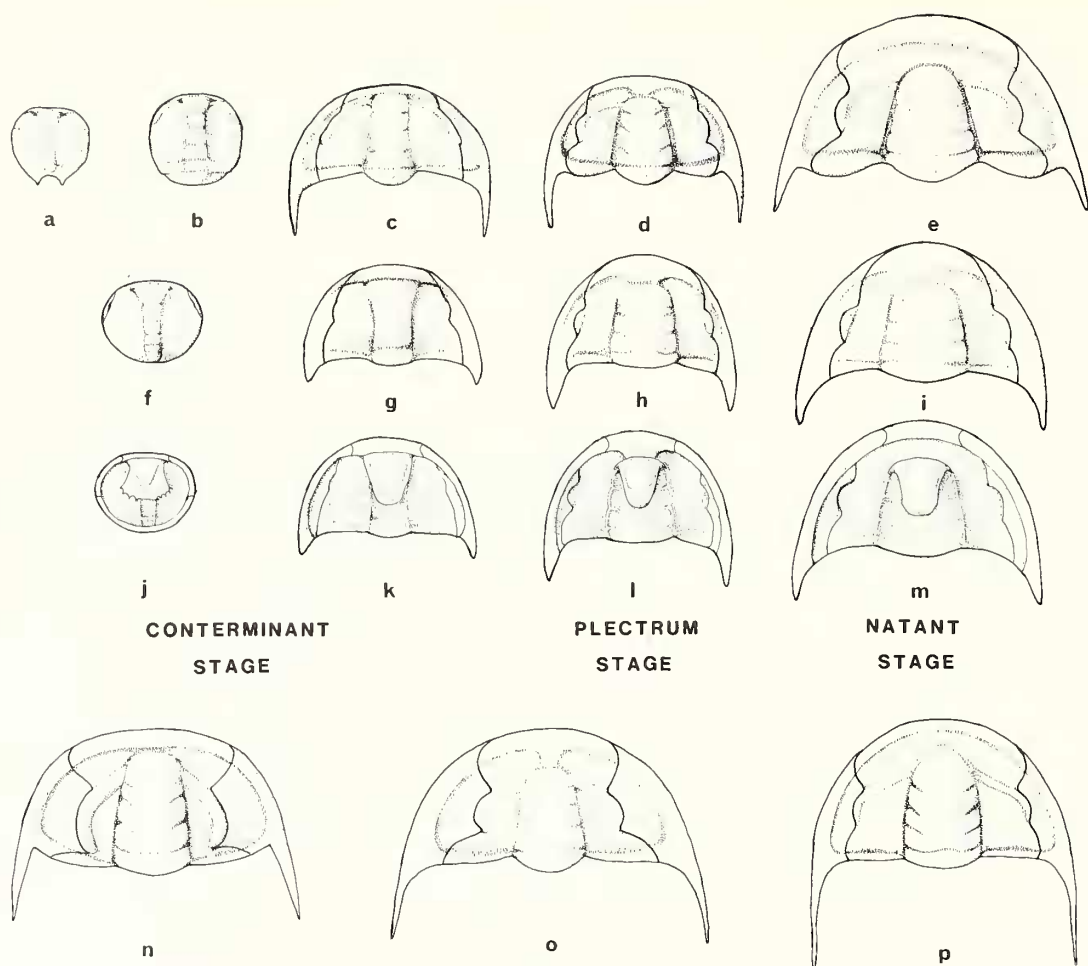
TEXT-FIG. 9. Natant hypostomal condition as a derived character. Ontogenies of typical ptychoparioids, showing change from conterminant to natant, by way of a plectrate stage. *a–e*, *Ehmaniella waptaensis* Rasetti (after Hu 1986, text-fig. 11), Middle Cambrian, Canada, dorsal views; *a*, small protaspis, ×20; *b*, large protaspis, ×16; *c*, meraspis cranidium *c*. ×15; *d*, late meraspis, ×5; *e*, holaspis, ×5. *f–m*, ontogeny of *Crassifimbra* (after Palmer 1958), Late Lower Cambrian, Nevada, dorsal (*f–i*) and ventral (*j–m*) views of comparable stages. The rostral form at the 'plectrum stage' is not yet described for this species, but is inferred from such specimens as that depicted by Zhang and Jell (1987, pl. 80, fig. 1 *n–p*); the ontogenetic series is matched by adult cranidial morphologies among Lower Cambrian trilobites, which may record the evolutionary steps involved in the origin of natant groups; *n*, *Redlichia* (after Zhang *et al.* 1980); *o*, *Dolerolenus* (after Rasetti, 1972); *p*, *Hamatolenus*.

Hence during ontogeny the hypostome of trilobites with adults having the natant hypostomal condition must have become separated from the doublure. How this may have happened in Ptychopariidae has already been well described in *Crassifimbra* (Palmer 1958) and can be inferred from the ontogeny of other 'generalized' ptychoparioids such as *Ehmaniella* (Hu 1984, 1986). Protaspides of such ptychoparioids are all very similar (Palmer 1962; Hu 1971; text-figs. 9, 10*h–m* herein) having a narrow axis with transverse annulations of varying inflation, the anterior of the axis expanding in width near the front margin of the protaspis. During the meraspis stage (text-fig. 9), a distinct frontal cranidial border appeared (e.g. Palmer 1958, pl. 26, fig. 4), with which the doublure

corresponds ventrally, but at this stage the glabella still reached the border, and it is a reasonable interpretation that the hypostome was attached and conterminant. Subsequent growth allows for the appearance of the preglabellar field, at first narrow, and widening during subsequent instars. This marks the separation of border from glabella, and presumably the detachment of hypostome from doublure, with the onset of the natant hypostomal condition. In both *Crassifimbra* and *Ehmaniella* this happens during the later meraspis. The conterminant stage is separated from the natant by a phase in which the border furrow curves towards the glabella as a plectrum (plectrum stage in text-fig. 9). In the ontogeny of *Sao* (Whittington *in* Moore 1959) the degree 1 meraspis was conterminant, the degree 6 meraspis natant. Thus the ontogeny (conterminant to natant) parallels the inferred phylogeny. Again this is consistent with the recognition of the natant condition as a synapomorphy. Adult trilobites representing the plectrum stage are described from several families (e.g. text-fig. 9). In those Ordovician forms known to be *secondarily* conterminant from phylogenetic analysis, there is no evidence to suggest that they went through a natant growth stage during ontogeny (e.g. Asaphidae; Tripp and Evitt 1986) and so the mature conterminant condition was attained by its retention and displacement into the adult, essentially a process of paedomorphosis. However in certain Cambrian genera there is evidence to suggest that there may still be an intervening natant phase of ontogenetic development (i.e. the sequence may run attached hypostome – free – secondarily attached). In *Auritama trilunata*, illustrated by Öpik (1967, pl. 15, figs. 3–6), a series of cranidia ranging through probable meraspis to large holaspis show a progressively widening border and reduced preglabellar field, the border being known to correspond with the cephalic doublure. It is not known whether the hypostomal attachment became secondarily conterminant in this species, although the close coincidence of border furrow and preglabellar furrow in the largest cranidium suggest that it may well have been so.
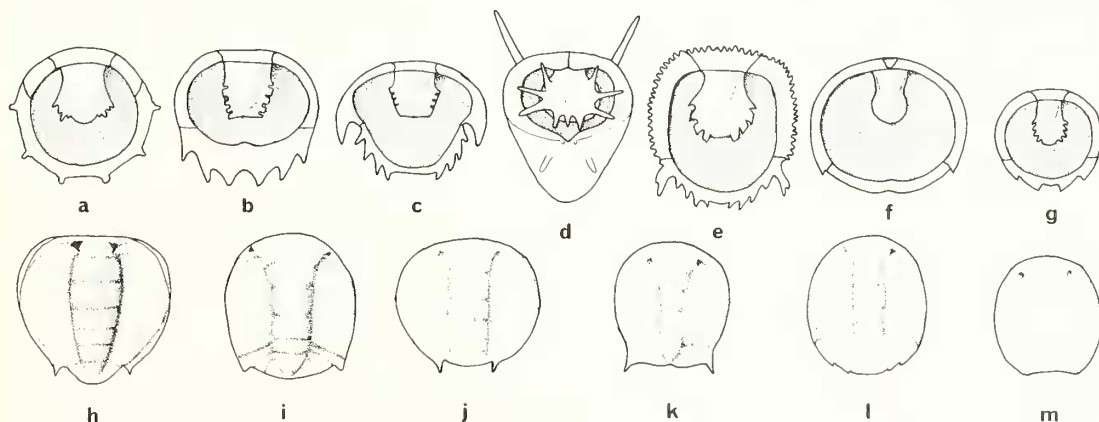
TEXT-FIG. 10. *a–g*, attachment of hypostome to doublure as the general condition in larval trilobites, illustrated by protaspides of major trilobite groups shown from the ventral side. a, Ptychopariina, *Aphelaspis* (after Palmer 1962); *b*, Lichida, *Acanthopyge* (after Chatterton 1971); *c*, Scutelluina, *Dentaloscutellum* (after Chatterton 1971); *d*, Asaphida, *Isotelus* (after Evitt, 1961); *e*, Phacopida (Calymenina), *Flexicalymene* (after Fortey and Chatterton 1988); *f*, Proetida, *Proetus* (after Chatterton 1971); *g*, generalized Ptychopariina, *Spencella* (after Fortey and Chatterton 1988). Not to scale. *h–m*, dorsal views of Cambrian libristomate protaspides of various families showing general (plesiomorphic) similarity, and frontal position of anterior pits indicating that the hypostome was attached to the doublure on the ventral surface. These protaspides are arranged in order of greater effacement from left to right. *h*, late protaspis of *Leptoplastus* (Olenidae) (after Whitworth 1970), ×60; *i*, late protaspis of *Welleraspis* (Catillicephalidae) (after Rasetti 1954), ×50; *j*, late protaspis of *Dytremacephalus* (Pterocephaliidae) (after Hu 1971, pl. 16, fig. 4), ×50; *k*, late protaspis of *Hardyoides* (Menomoniidae) (after Palmer 1962), ×60; *l*, late protaspis of *Dunderbergia* (Alokistocaridae) (after Hu 1971, pl. 15, fig. 8), ×50; *m*, early protaspis of *Glyphaspis* (Anomocaridae) (after Hu 1971, pl. 11, figs. 1 and 2), ×50.

Relatively little is known about early Cambrian redlichiid ontogeny. Kobayashi and Kato (1951) described the ontogeny of *Relichia chinensis* Walcott, and figured an early conterminant stage. This has been augmented by Zhang *et al.* (1980) who have described ontogenetic series of *Redlichia takooensis* Lu and *R.* (*Pteroredlichia*) *murakamii* Resser and Endo, including a protaspis stage. By early meraspis stage (Zhang *et al.* 1980, pl. 23, figs. 5–7) there was a distinct, ledge-like anterior border, and it is likely that the hypostome was conterminant. As in olenellids *Redlichia* larvae show well-developed palpebro-ocular ridges which curve strongly backwards. Palmer (1957) described the ontogeny of *Olenellus*, which apparently lacked a protaspis stage; by the early meraspis hypostome and doublure were connected only by a median prong, which appears to be the same condition as pertained in adult olenellids having a preglabellar field. Palmer and Halley (1979) described the ontogeny of another olenellid, *Bristolia*, in which it seems likely that the conterminant condition pertained throughout ontogeny, because the border and preglabellar furrow remain in contact. Because the redlichiids rather than the olenellids are likely to be the primitive sister group of the ptychoparioids the ontogeny of olenellids is less relevant to trilobites having natant hypostomal condition. The familiar mid-Cambrian redlichiine *Paradoxides* is presumably conterminant throughout ontogeny. The ontogenies of early representatives of trilobites with natant hypostomal condition will prove relevant to the morphogenesis of the structures involved, but little is known at present. A critical group may prove to be the Protolenidae. *Protolenus* itself was probably natant in the adult, with the glabella falling well short of the border; closely related genera such as *Myopsolenus* certainly were natant, as shown by specimens showing the inner margin of the cephalic doublure (e.g. Bassett *et al.* 1976, pl. 1, fig. 1) which is well-removed from the preglabellar furrow. Romanenko (1977, pl. 13, figs. 3–5) described *Protolenoides fasciferrus*, and included a figure of a meraspide cranidium which appears to be of the usual ptychoparioid type, and hence presumably had an attached hypostome. Small, submature cranidia of the same species show a strong plectrum extending to the glabellar front. If this represents the dorsal expression of a backward extension of the rostrum then it might be suggested that the hypostome was still in primary conterminant attachment mode. The plectrum is less distinct in fragmentary larger cranidia. Plectra are also present in some other protolenids (*Bergeroniaspis*, *Olekmaspis*), and in Dolerolenidae (*Dolerolenus* – see Rasetti 1972, pl. 15, fig. 4). I would speculate that this plectrate condition might represent the transition between primary conterminant and natant hypostomal condition as shown in text-figure 9. Interestingly, it parallels the situation in *Proceratopyge* (e.g. Rushton 1983, text-fig. 6*b*; Jago 1987; text-fig. 3*b* herein) in which the reverse was happening: as the hypostome achieved *secondary* conterminant hypostomal condition a plectrum is developed dorsally corresponding with a backward extension of the cephalic doublure (in this case including a median suture). The ontogeny of the Corynexochida, in which the hypostome remained attached to the doublure throughout growth, was described by Robison (1967).

Stratigraphic evidence for natant condition as a derived character

International correlation of early Cambrian rocks is still controversial. However, in no section with a relatively complete sequence does a ptychoparioid appear first below a redlichiid (Brasier 1989). Hence so far as it goes the stratigraphic record is in accord with the proposed character polarity.

To summarize, ontogeny and stratigraphy confirms the conclusion drawn from comparison with other arthropods, and from the phylogenetic analysis of trilobite relationships used by previous authors, that an attached hypostome is primitive and the natant hypostomal condition a derived character. It is concluded that *those trilobites having natant hypostomal condition can be regarded as constituting a monophyletic group*. Those trilobites which were *primitively* natant, but secondarily conterminant, such as were discussed above, belong within the same group.

Distribution of natant hypostomal condition in the various trilobite families

There now follows an inventory of trilobite families in which the natant hypostomal condition occurs, or can be reasonably inferred to occur, with documentation. Some examples are illustrated

on Plate 1; for most others a literature reference is given, either showing the hypostome as it fell into the forward part of the glabella upon decay of the soft parts, separated from the cephalic doublure, or showing that the extent of the cephalic doublure fell short of the preglabellar furrow. Some modes of hypostomal attachment were described in detail by Whittington (1988*a*, *b*). The list is not exhaustive, in that one or two examples are sufficient for each family, and there may be additional families for which I have not found evidence. For convenience families are arranged alphabetically. Families are accepted uncritically, although many are not satisfactory, monophyletic taxa. Even so I cannot accept Raymondinidae, which is an absurdly heterogeneous collection of genera in the *Treatise*.

Agraulidae. *Agraulos* was discussed in detail by Whittington 1988*a*.

Alokistocaridae. See *Elrathia* (Pl. 1, fig. 6).

Anomocaridae. See discussion in Fortey and Chatterton (1988); *Anomocarioides limbatus* (Egorova *et al.* 1982, pl. 44, fig. 2).

Andrarinidae. A somewhat doubtful taxon. Dean (1972) illustrated narrow cephalic doublure of *Holasaphus*, which shows likelihood of natant hypostomal condition. Although *Holasaphus* was placed in this family by Howell (*in* Moore 1959), it was assigned with question to Ptychopariidae by Dean.

Asaphiscidae. *Blainia*, see Pl. 1, figs. 2, 8.

Aulacopleuridae. Natant condition can be inferred on *Aulacopleura* with narrow and tubular cephalic doublure and wide preglabellar field.

Auritamiidae. See ontogenetic series of *Auritama trilunata* (Öpik 1967, pl. 15, figs. 3–6.) and discussion above (p. 547).

Bathyuridae. See discussion above (p. 538); most bathyurids are regarded as likely to have been natant except *Bathyurus* (Whittington, 1988*b*).

Cedariidae. *Cedaria* (Pl. 1, fig. 3).

Conocoryphidae. Probably a polyphyletic family, united only by secondary blindness. *Conocoryphe* itself discussed in detail by Whittington (1988*a*).

Dimeropygidae. This family is problematic, in that *Dimeropyge* has a curious rostral plate (Tripp and Evitt 1983, pl. 33, fig. 11; Chatterton and Ludvigsen 1976, fig. 8) with a prong-like extension which may have engaged with the unusually small hypostome (which has reduced anterior wings). If this is so it qualifies as a unique form of (derived) hypostome attachment, and is neither natant nor conventionally secondarily conterminant. On the other hand I have searched inside entire cephalic shields of early dimeropygids such as *Ischyrotoma anataphra* Fortey, 1979 without finding any sign of an attached hypostome, and I think it likely that these early forms were natant.

Dokimocephalidae. Little known of ventral surface. Narrow doublure of free cheeks shown in *Wuhnia* by Zhang and Jell (1987, pl. 119, fig. 5) and natant condition likely in this member of the family.

Ellipsocephalidae. Šnajdr (1958) has illustrated the cephalic doublure of the type species of *Ellipsocephalus*, which demonstrates the likelihood of a gap between hypostome and doublure.

Hapalopleuridae. *Skjarella* sp., a new discovery in the Tremadoc of Shropshire by myself and R. M. Owens (in prep.) shows natant condition in entire specimen with hypostome in place.

Idahoiidae. *Saratogia*, narrow width of genal doublure illustrated by Ludvigsen and Westrop (1983, pl. 8, fig. 10); if this followed border furrow on cranidium then natant condition pertained.

Loganopeltidae and Harpididae. Lower lamella in *Harpides* falls well short of glabellar front (holotype of *H. grimmi* Barrande, 1872 shows hypostome in place). These two families are united by some authors.

Lonchocephalidae. Rasetti (1954, pl. 62, fig. 13) illustrated narrow genal doublure, and rostral suture of *Welleraspis swartzi*. It is possible that some lonchocephalids lacking preglabellar field were secondarily conterminant (*cf.* Whittington 1988*a*).

Marjumiidae. See Robison (1964, pl. 10, figs. 10–15) for silicified specimens of *Modocia* showing how doublure falls short of preglabellar furrow.

Menomoniidae. *Bolaspidella* discussed by Whittington 1988*a*.

Nepeiidae. *Penarosa netenta*, see Jell (1977, especially pl. 21, figs. 5, 7).

Olenidae. Diagnosis in Nikolaisen and Henningsmoen 1985; *Peltura* see Henningsmoen (1957, pl. 26, fig. 2); *Porterfieldia* (Fortey and Owens 1978, pl. 1, fig. 5); *Parabolinella* (Whittington 1988*a*); *Hypermecaspis* (Pl. 1, fig. 1). Some of the *in situ* hypostomes seem to be too small to have been attached by the anterior hypostomal wings as suggested by Whittington 1988*a*. Some derived forms which have lost the preglabellar field (*Triarthrus* see Whittington *and* Almond 1987) may have become secondarily conterminant.

Papyriaspididae. Doublure of free cheek of *Papyriaspis lanceola* figured by Öpik (1961, pl. 17, fig. 3).

Parabolinoididae. See, for example, Westrop (1986, pl. 18, fig. 18) for narrow genal doublure coinciding with border in *Orygmaspis* (*Parabolinoides*) species with wide preglabellar field.

Proetidae. *Proetus* (Pl. 1, fig. 7) and *Decoroproetus*, see Owens (1973) for specimens preserved from ventral side with hypostomes nearly *in situ*.

Protolenidae. *Hamatolenus* see Bassett *et al.* 1976, and comments above.

Pterocephaliidae. *Strigitambus? blepharina* (Palmer 1968, pl. 16, fig. 15), *Litocephalus* (Palmer 1960, pl. 8, figs. 13, 16). See also discussion in Fortey and Chatterton 1988, which excludes *Aphelaspis* (also natant) from this family.

Ptychopariidae. *Ptychoparia striata* (see Whittington 1988*a*); *Asthenopsis* (see Jell 1978*a*). Šnajdr (1958, pl. 40, fig. 3) showed *Ptychoparia* hypostome in near-life position.

Remopleuridacea. *Richardsonella* (see Palmer 1968, pl. 14, fig. 8); *Elkanaspis* (see Ludvigsen 1982 for silicified specimens showing narrow cephalic doublure combined with wide preglabellar field).

Solenopleuridae. *Sao*, discussed in Whittington 1988*a*.

Trinucleidae. Statement in Hughes *et al.* (1975, p. 541); Whittington (1988*b*, p. 328).

This long list proves two important points:

1. If the natant hypostomal condition defines a monophyletic group as argued above, it is retained in a variety of families within that group – it is generally a stable character.

2. Within this group it is also a primitive character, being shared with the common ancestor of the group. This means that it is of *no consequence in defining phylogenetically based subgroups*. This is the usual situation where a synapomorphy becomes symplesiomorphic at the next level in the taxonomic hierarchy (Eldredge and Cracraft 1982). Hence within the group defined by having natant hypostomal condition, any subgroups have to be defined on other, derived characters.

This means that natant hypostomal condition is of use in suggesting common ancestry, but we must look to other characters to define natural groups within this great assemblage of trilobites. Those groups (currently Asaphina, Proetida) with secondarily conterminant or impendent hypostomal condition belong within the overall natant group, and have to be defined on other derived characters – for example, the Asaphina are defined by having a median suture – and the fact that early members of the group have natant hypostomal condition while later ones generally have attached hypostomes (Fortey and Chatterton 1988) supports their common ancestry, but does not greatly help with the definition of the group. A definition of Proetida is given below.
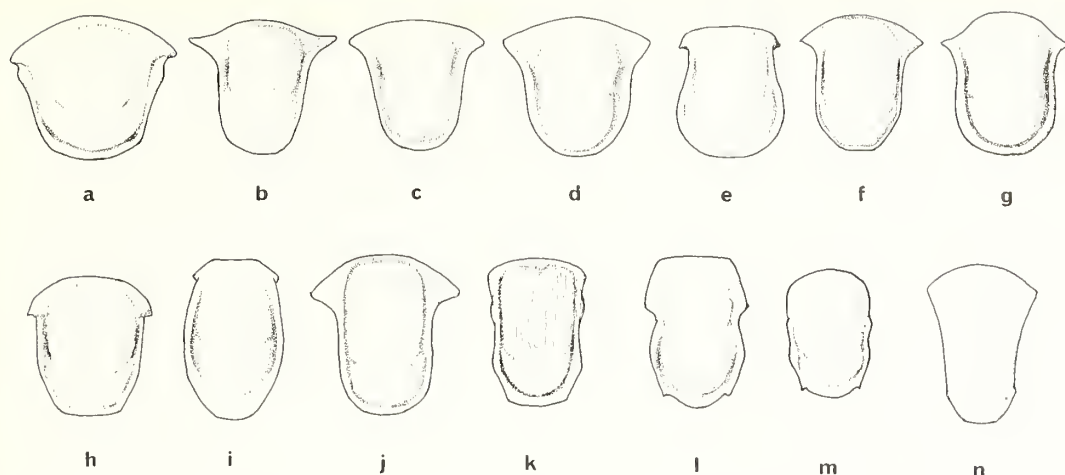
If the natant hypostomal condition is correctly regarded as a synapomorphy then the natural group having it, or only secondarily losing it, needs a name. For this group I propose the name **Libristoma**. The taxonomic status of the Libristoma is discussed in more detail below; it is a more inclusive group even than the Order Ptychopariida.

HYPOSTOME ATTACHMENT AND HYPOSTOME SPECIALIZATION

One of the consequences of the natant hypostomal condition seems to have been that, upon the death of the trilobite, or during moulting, the hypostome was easily separated from the rest of the exoskeleton. I do not think it is a coincidence that most of the families listed above have very few species for which the hypostome is definitely assigned. Of dozens of species of Ordovician trinucleids only two to my knowledge have hypostomes associated, and the figure is similar for many Cambrian families, and some (e.g. Dokimocephalidae) apparently have no hypostome yet associated. Conversely, unassigned hypostomes, all very similar, are often figured at the end of monographs on Cambrian trilobites (e.g. Palmer 1960, pl. 11). Cambrian families with conterminant hypostomal condition, such as Redlichiidae, Paradoxididae or Corynexochidae, have numerous species with definite assignment of hypostomes. The same applies to those families (Asaphidae, Nileidae) in which secondary hypostomal attachment has occurred. Nonetheless in natant families when the right kind of ventral-side-up preservation occurs the hypostomes are found in the appropriate position, and I see no grounds to suppose that there were species which lacked hypostomes altogether.

On gathering together information on the hypostomes which *have* been assigned to trilobites

TEXT-FIG. 11. The conservative morphology of hypostomes from trilobites having natant hypostomal condition, illustrated by hypostomes of species belonging to several families and ranging in age from Lower Cambrian to Carboniferous (top left to bottom right). *a*, yinitid redlichiid *Drepanopyge* (after Zhang *et al.* 1980, pl. 51, fig. 9), showing how this primitive morphology is retained in natant trilobites, ×2. Natant hypostomes: *b*, *Crassifimbra* (Ptychopariidae), Lower Cambrian (after Palmer 1958, pl. 25, fig. 13), ×10; *c*, *Conocoryphe* (Conocoryphidae), Middle Cambrian (after Šnajdr 1958, pl. 34, fig. 4), ×4; *d*, *Ptychoparia striata* (Ptychopariidae), Middle Cambrian, (after Šnajdr 1958, pl. 40, figs. 3, 5), ×2·5; *e*, *Dunderbergia* (Alokistocaridae), Upper Cambrian (after Hu 1971, pl. 15, fig. 30), ×10; *f*, *Aphelaspis* (regarded as Pterocephaliidae), Upper Cambrian (after Rasetti 1965, pl. 20, fig. 9), ×5; *g*, a hystricurid, early Ordovician (after Ross 1951, pl. 19, fig. 3), ×9; *h*, *Parabolinella* (Olenidae), early Ordovician, ×4; *i*, *Bathyurellus* (Bathyuridae), early Ordovician (after Fortey 1979, pl. 31, fig. 9), ×3; *j*, *Paraproetus*, (Proetidae), late Ordovician (after Owens 1973, pl. 12, figs. 12*a* and *b*), ×7; *k*, *Proetus* (Proetidae), Silurian (after Owens 1973, pl. 4, fig. 19), ×4; *l*, *Koneprusites* (Proetidae), Devonian (after Šnajdr 1980, pl. 51, fig. 10), ×6; *m*, *Voigtaspis* (Proetidae), Devonian (after Šnajdr 1980, pl. 52, fig. 11), ×3; *n*, *Phillipsia* (Phillipsiidae), Carboniferous (after Woodward 1883, pl. 2, fig. 6), ×3.

having natant hypostomal condition another fact becomes clear. The hypostomes of trilobites with natant hypostomal condition tend to be as similar as they are unremarkable (Whittington 1988*a*, p. 604; text-fig. 11 herein). What they share is an elongate (sag.) oval middle body, carrying a pair of usually rather short middle furrows often posterolaterally placed; rather narrow (tr) lateral borders, and a rounded to transverse posterior border without a fork, or other marginal modification; a pair of small posterolateral spines may or may not be present. Hypostomes of this kind can be found from the Lower Cambrian to the Upper Palaeozoic. The hypostomes of some redlichiid and dolerolenid trilobites are virtually identical (e.g. *Dolerolenus*, see Rasetti 1972, pl. 16) and the obvious inference is that this 'ptychoparioid' hypostome is a retained primitive character. As the redlichiid ancestor of the Libristoma acquired the natant hypostomal condition, the hypostome became, as it were, morphologically frozen. Surface sculpture on many of these hypostomes was lacking, or at most finely granulate, and only became at all complex on some proetids. The cephalic doublures of most 'ptychoparioids' carry terrace ridges. We can contrast the conservatism of the natant hypostome with the new features in morphology that arise in secondarily conterminant and impendent hypostomes (text-fig. 12). Posterolateral hypostomal borders can become very wide (Nileidae); posterior forks can develop (most Asaphidae, *Hypodicranotus* in the Remopleurididae); the overall shape can become greatly elongate (Brachymetopidae) or transverse (Cyclopygidae); maculae may become prominent (*Remopleurides*) or absent (the cyclopygid *Degamella*). The terrace ridges hitherto largely confined to the cephalic doublure appear to 'spread onto' the hypostome and may be as prominent, or even more prominent, as they are upon the
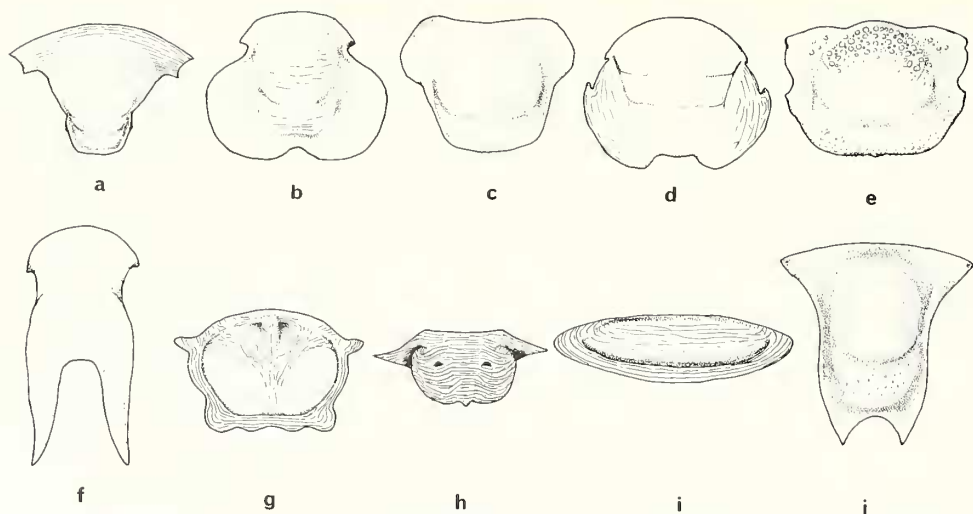
TEXT-FIG. 12. Hypostomes of trilobites in which the hypostome was attached to the doublure in either impendent or conterminant mode, showing various kinds of specialization, in contrast to the natant hypostomes shown in text-fig. 11. *a–e* shows primary conterminant examples, as interpreted herein; *f–i* are secondarily conterminant hypostomes belonging to Libristoma; *j* may be secondarily conterminant (see discussion of Phacopida, p. 565). *a, Fieldaspis* (Corynexochida), Middle Cambrian (after Rasetti 1951, pl. 16, fig. 17), ×1·5; *b, Palaeadotes* (Damesallacea), Cambrian, Mindyallan (after Öpik 1967, pl. 50, fig. 3), ×4; *c,* illaenid (Illaenacea), Middle Ordovician (after Whittington 1963, pl. 18, fig. 4), ×3; *d, Amphilichas* (Lichida), Middle Ordovician (after Tripp and Evitt 1981, pl. 2, fig. 28), ×6; *e, Primaspis* (Odontopleurida), Silurian (after Chatterton and Perry 1983, pl. 5, fig. 5), ×6; *f, Lycophron* (Asaphacea), early Ordovician (after Fortey and Shergold 1984, pl. 43, fig. 5), ×3; *g, Remopleurides* (Remopleuridacea), Middle Ordovician (after Whittington 1959, pl. 17, fig. 18), ×6; *h, Symphysurus* (Cyclopygacea), Middle Ordovician (after Fortey 1986, fig. 2), x 1; *i, Degamella* (Cyclopygacea), early Ordovician (after Fortey and Owens 1987, fig. 38*d*), ×2·5; *j, Salterocoryphe* (Calymenacea), Middle Ordovician (after Hammann 1983, pl. 11, fig. 107), ×6.

doublure. Such derived hypostomal characters at once become of taxonomic use, in defining families, genera, or even species (asaphids are often best distinguished by hypostomal details). Hence, natant hypostomes are of a generalized type and change little; attached hypostomes are rapidly deployed into a variety of shapes and are as variable as any dorsal morphological features. This has to be connected with the function of the hypostome in the life habits of the trilobites included in the Libristoma.

If these facts are easily stated the possible explanations of the facts quickly become speculative. What is certain is that the natant condition was both widespread and enduring. As a derived character it was connected with life habits that the trilobites could ubiquitously and successfully prosecute from the Cambrian to the Carboniferous, and it is unlikely, therefore, that it was related to any peculiar specialization, such as parasitism. Because the hypostome remains remarkably conservative it is possible to suggest that it was not actively involved in the mastication of food, and this is supported by the lack of the kind of buttressed attachment found in the conterminant and impendent hypostomal conditions. So it seems reasonable to argue further that it was the very flexibility of the hypostomal attachment that was of adaptive importance. If Whittington's (1988*a*) view of the relationship between anterior hypostomal wings and anterior pits (or the homologous points in the axial furrows) is correct then the hypostome was tethered rather than entirely free-lying, but that the attachment was not rigid is shown by the ease with which it becomes displaced on death to produce specimens like that shown in Pl. 1, fig. 7.

If the mouth lay at the back end of the hypostome it is not unreasonable to assume that the ovate middle body of the hypostome corresponded with some kind of foregut above it. In this case

flexibility of the hypostome would mean that the foregut might be manipulated by the hypostome itself. If we further assume that the hypostome was 'tethered' by the anterior wings this movement would be confined to up-and-down movement of the adoral margin: more precisely the movement would be upwards-and-backwards because of the tethering at the anterior end of the hypostome. It would be a scooping motion. The musculature necessary to do this would be appropriately sited if it attached to the middle furrows. It does not seem likely that the muscles were particularly powerful because the middle furrows are usually rather weakly defined. Hence it is likely that if the hypostome functioned in this scoop-like fashion the particles handled were small. This could either mean that the natant trilobite lived on small organic particles extracted from the sediment by the setate bases of the coxae (cf. Whittington and Almond 1987) and then passed forwards along the ventral 'food groove', or that the trilobite directly ingested partially sorted sediment, the process of nutrient extraction being carried out in the gut. In any case it seems unlikely that natant trilobites handled large prey. The scooping motion of the hypostome/foregut could have functioned in shovelling a considerable quantity of sediment and organic material for digestive processing. It may be relevant that many 'ptychoparioid' (Ptychopariidae, Olenidae, aphelaspids, etc.) trilobites have well-developed caecal networks, some of which have been interpreted as intestinal diverticulae (other workers claim these as arterial, see Jell 1974). But the conservatism of the natant hypostome attests to it not being directly involved with the manipulation and processing of food, however the food was derived.

As soon as the hypostome became secondarily conterminant or impendent specializations appeared. Whittington (1988*a*, *b*) has demonstrated that the hypostomes in all cases of conterminant or impendent attachment he examined were rigidly attached at the sutural junction with the doublure. This implies a functional difference compared with the natant condition. Such hypostomes cannot be involved with the shovelling of food forwards, but it becomes possible for them to become part of the mechanism of manipulating and processing the food gathered. The powerful buttressing of the hypostomal wings and doublure that happens in, for example, asaphids and nileids implies that mechanical strength was important in this function. Certain species with attached hypostomes have conspicuous rasps on the adoral part of the hypostomal margin: this is shown by the odontopleurids discussed by Chatterton and Perry (1985), and by the asaphid *Isotelus* (text-fig. 3*e*, p. 534). Such rasps could have functioned in concert with the limbs in the shredding or comminution of large food particles. It seems likely to me that the Libristoma having predatory habits were also those having secondary conterminant or impendent hypostomes. The special-izations of the hypostomes were the result of the various stratagems evolved to deal with bulkier food items, including prey in at least some species. The function of rasps does not pose an interpretative problem, but many of the other specializations do. Forks, or lateral spine-like processes, are developed on many conterminant hypostomes, both primary and secondary (*Paradoxides*, calymenids, asaphids, some remopleuridids). In asaphids the fork extended to either side of the mouth and may carry strong terrace ridges on its outer surface (e.g. Fortey 1979, pl. 23, fig. 4) – could these have also helped in manipulating food? The maculae behind the middle furrows on asaphids and nileids are modified, bevelled areas, and their function is not resolved, but if the hypostomal retractor muscles remained they must have taken on a different function. Remopleuridids have enormously extended maculae the function of which is unknown. The spread of terrace ridges from the cephalic doublure onto the anterior part of the middle body of the hypostome in the secondarily attached condition means that this part of the hypostome has become, functionally speaking, part of the antero-venter. The function of terrace ridge systems in trilobites is not without controversy, but anterior cephalic ones probably functioned as sediment grippers in some instances (Schmalfuss 1981; Fortey 1986). In the secondarily conterminant families these changes from natant hypostome morphology happened over an early Ordovician period of perhaps ten million years. The functional interpretation of the specializations of attached hypostomes is a fruitful field for further research. For the moment it is only possible to contrast these morphological excursions with the conservatism of hypostomes separated from the doublure, for which one presumes a single function sufficed for several hundred million years.

CLASSIFICATION OF AGNOSTIDA

The Agnostida are usually understood to comprise the agnostids themselves, Suborder Agnostina, and the eodiscids and pagetiids (suborder Eodiscina *sensu* Moore (*in* Moore 1959); superfamily Eodiscoidea *sensu* Jell (1975)). There is now much evidence that the hypostome of the Agnostida was not attached ventrally (text-fig. 13). The apparently natant condition in Eodiscina has been discussed by Jell (1975, pl. 1, fig. 1) and Whittington (1988*a*), and is now known in several members of the Agnostina (Robison 1972*a*; Jell 1975, pl. 1, fig. 3; Müller and Walossek 1987; Robison 1988), and there is no reason to suppose it was other than general.

a **b** **c**
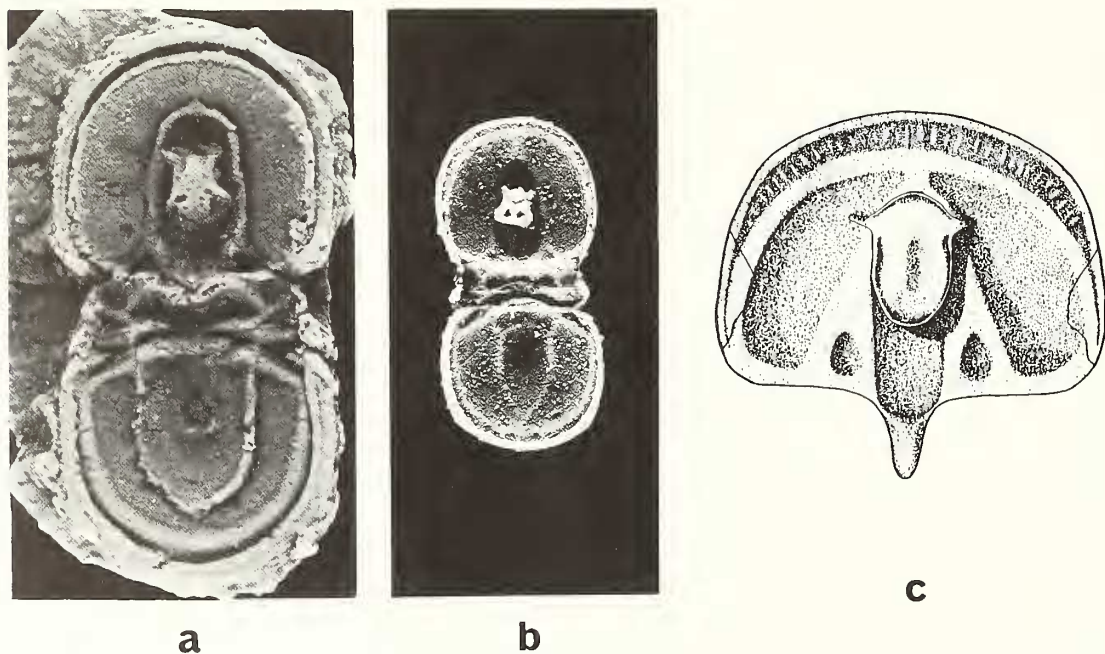
TEXT-FIG. 13. Natant hypostomal condition in Agnostida, showing no indication of rostrum. Agnostina: *a*, *Peronopsis ferox* (Tullberg) (Robison 1972*a*, fig. 2*d*) × 21; *b*, *Onymagnostus seminula* (Whitehouse), (Robison 1982, pl. 4, fig. 5*b*), × 10; photographs kindly supplied by R. A. Robison. Eodiscina: *c*, *Pagetia* cephalic shield from underside (after Jell 1980, pl. 1, fig. 1).

When I first recognized the natant condition as a synapomorphy I had considered that the agnostids should belong in the same monophyletic group as libristomates because of their unattached hypostome. This was wrong. The natant condition in Agnostida is **not** homologous with that in Libristoma. Recognition of this also serves to place the Agnostida within the Trilobita (text-fig. 14), which has been a long-standing problem. It is necessary to discuss this before considering the ptychoparioids further.

Much more is known of agnostid anatomy following Müller and Walossek's (1987) magnificent work. Obvious agnostoid specializations have led them to be classified separately from the rest of the Trilobita (Miomera of Jaekel 1909). However, the original emphasis placed on the paucity of thoracic segments does not bear scrutiny because it is now known that several other groups of trilobites may include species with only two or three thoracic segments, for example Corynexochida (Robison and Campbell 1974) and Raphiophoridae (Zhang 1980). Small numbers of segments result from a change in developmental programme (cf. McNamara 1986), and it is not a character of great weight, taxonomically speaking, although it is stable in Agnostina. The fact remains that
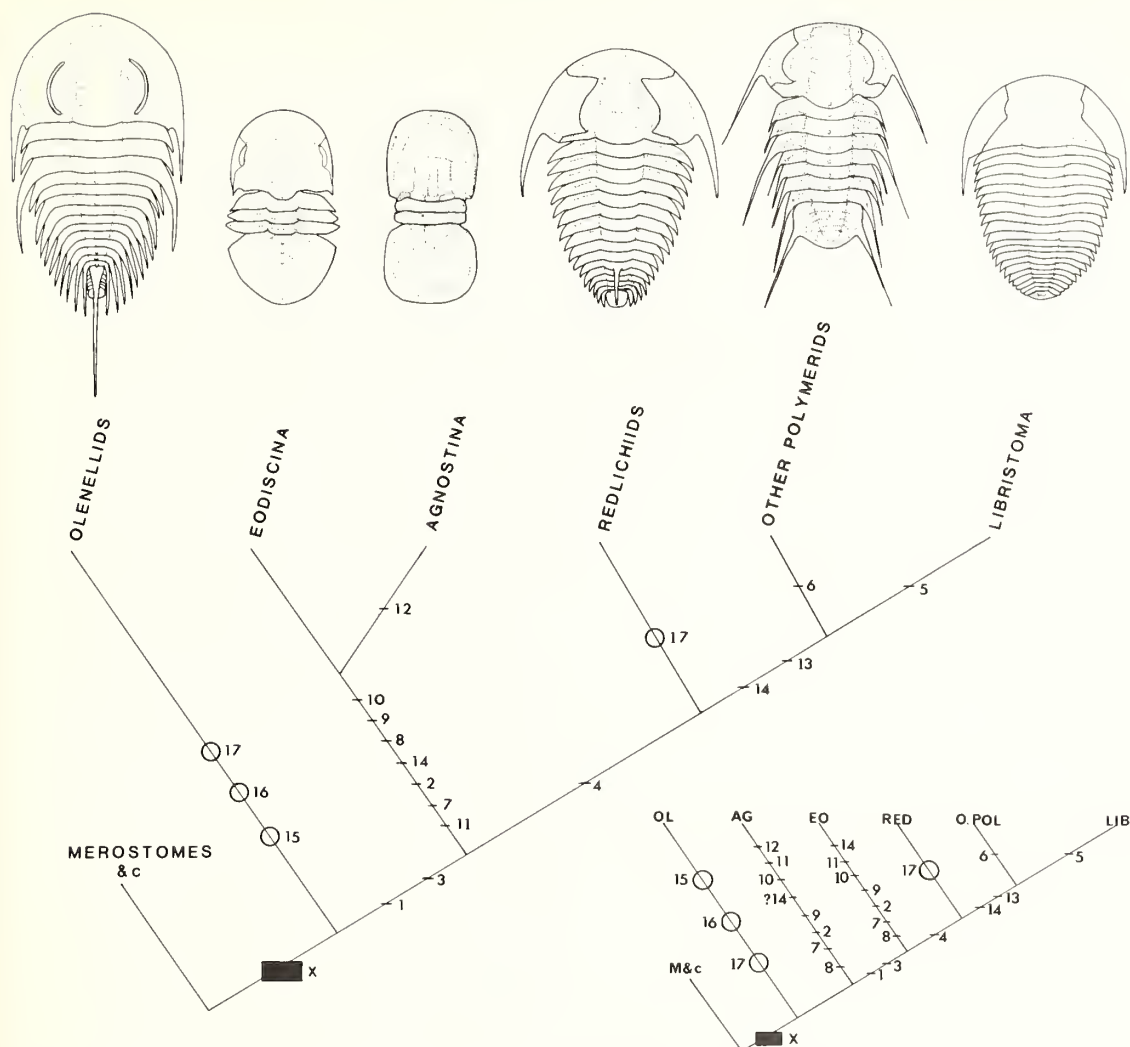
TEXT-FIG. 14. Hypothesis of relationships placing Agnostida and Libristoma in the Trilobita as a whole. Smaller inset shows a second hypothesis which is not favoured by the author. The relationship of Libristoma to the group termed 'other polymerids' is not resolved. 'Other polymerids' comprises primary conterminant non-redlichiid trilobites: Corynexochida, Lichida, Odontopleurida, Scutelluina as discussed in text, and may not be a natural group, Derived characters are: X, combination of seven, possibly nine, synapomorphies of olenellids and other trilobites as discussed by Fortey and Whittington (1989) (presence of a pygidium; rostral plate; calcite eye lens structure; calcite cuticle; circum-ocular sutures in adult; eye ridges; hypostome with anterior wing directed dorsally to anterior pit; and possibly terrace ridges on doublure and spinose margin of larval hypostome); 1, acquisition of dorsal ecdysial sutures; 2, reduction in thoracic segment number to three or fewer; 3, acquisition of a calcified protaspis; 4, connective sutures present (section of doublure included on free cheek); 5, natant hypostomal condition; 6, glabella sharply truncated at ledge-like border; 7, loss of calcification of olenellid-like rostral plate; 8, occipital width greatly exceeds (tr.) width of preoccipital glabella (expressed as triangular 'basal lobes' in Agnostina); 9, broad, 'rolled' cephalic border; 10, cephalic shield long (sag.) (maximum width often in front of posterior margin); 11, genal spines reduced or absent; 12, cephalothoracic aperture; 13, protaspis/early meraspis eye ridges close to anterior margin ('ptychopariid style' protaspis); 14, fulcrum-and-facet thoracic articulation (flange-like articulation primitively present in olenellids and at least some redlichiids, position of acquisition of advanced articulation may be oversimplified here – probably accompanied by the capacity to enrol fully). Circles, some plesiomorphic characters: 15, dorsal sutures lacking; 16, rostral plate extending around ventral cephalic margin; 17, olenelloid glabella form (elongate, fusiform with round to acuminate frontal lobe). The illustrated genera are only token representatives of their groups, and not necessarily those from which coding was made.

the Agnostina are the most specialized of trilobites, possibly being planktic (Robison 1972*b*) and spending much of their life in the enrolled condition, according to Müller and Walossek (1987). This is not, however, relevant to their classification within the trilobites, which has to be based on shared characters rather than distinctive autapomorphies. Their peculiarities have tended to dominate the view about how they should be classified, for example: they 'are best treated within the Trilobita at present but...having a separate position within them' (Müller and Walossek 1987, p. 54).

The relationships of the Agnostida suggested here are shown on the cladogram (text-fig. 14). This places them firmly within the Trilobita, between the Olenellida and Redlichiida. If the reasons advanced by Fortey and Whittington (1989) for the olenelloids as the most primitive trilobites are accepted, this is the preferred position for the agnostoids based on the characters I consider relevant to the problem.

The reasons for this phylogenetic position are threefold:

1. Students of Eodiscina agree that this group is related to Agnostina, of which they may be the primitive sister group (Jell 1975; Zhang *et al.* 1980). According to Zhang *et al.* (1980, text-fig. 7) two different groups of agnostids may have been closely related to different eodiscids – implying that the latter is a paraphyletic group and the former polyphyletic. Howsoever these relationships are worked out in detail, within the Eodiscina as understood at present there appear to be a series of 'intermediates' spanning some of the gaps between pagetiid organization and agnostid organization: three and two segmented species within the same genus (*Pagetia* as discussed by Jell 1975); blind eodiscids otherwise with pagetiid features (see Rasetti 1966); and some eodiscids with pre-occipital median tubercles on the glabella (*Serrodiscus* and *Ladadiscus*, see Rushton 1966, text-figs. 3, 9). The agnostid hypostome is so far unique in construction (Robison 1972*a*) with its window-like openings, although according to Müller and Walossek (1987) this may only be a matter of cuticular thinning (see also Robison 1988, fig. 9). The cephalothoracic aperture (a gap between the thoracic axis and cephalon in the enrolled state produced by the absence of the articulating half-ring on the first thoracic segment) is considered to be a good apomorphic character of Agnostina. The hypostome of *Pagetia* is no different from the generalized 'ptychoparioid' hypostomes shown on text-fig. 11 (Jell 1975, pl. 28, figs. 1 and 2). Hence, for comparative purposes, the most primitive pagetiids are probably the best candidates for comparison with other trilobites to determine the relationships of Agnostida. They have dorsal facial sutures. The presence of such sutures was considered by Fortey and Whittington (1989) to define a clade of 'higher' (i.e. non-olenelloid) trilobites, and most authors agree (Bergström 1973; Lauterbach 1980) on the peculiarity of this character in arthropod phylogeny.

2. Redlichiida, and all other trilobites, other than olenelloids and Agnostida, have a rostral plate bounded laterally by connective sutures – or if the rostral plate has been lost (e.g. to produce fused cheeks) it is known that their ancestors had such a rostral plate. In ventral view free cheeks of this group show a truncated section of doublure. Olenelloids have a broad crescentic rostral plate, without connective sutures. If the olenelloids, on other criteria, are the most primitive trilobites, this form of rostral plate is also primitive. Ventral-side up preservation of numerous Agnostida, including those with hypostomes in place (text-fig. 13), show no sign of a rostral plate. The primitive agnostoids with dorsal sutures included in Pagetiidae do not show that part of the genal doublure bounded by connective sutures. Hence, the rostral form must have been as in olenelloids, but calcification has been lost (text-fig. 15). This is confirmed by an example where it appears to have been silicified in one of the youngest agnostids (Middle Ordovician, Hunt 1966), but still retains olenelloid form. The loss of calcification of the (olenelloid) rostral plate affords an autapomorphy defining the Agnostida, one which is unique in the Trilobita.

3. It follows that the unattached condition of the hypostome in the Agnostida is the result of loss of the rostral plate and not the same as in the Libristoma. Individual agnostoid ontogenies described by Jell (1975) and Rushton (1966) show that the preglabellar field became progressively longer during ontogeny. It is suggested that the most primitive member of the Eodiscina could be such a species as *Sinodiscus changyanensis* S. G. Zhang *in* Zhang *et al.*, 1980, in which dorsal furrows and eye ridges are well-defined (as in olenellids) and the preglabellar field is short.

a   b   c   d
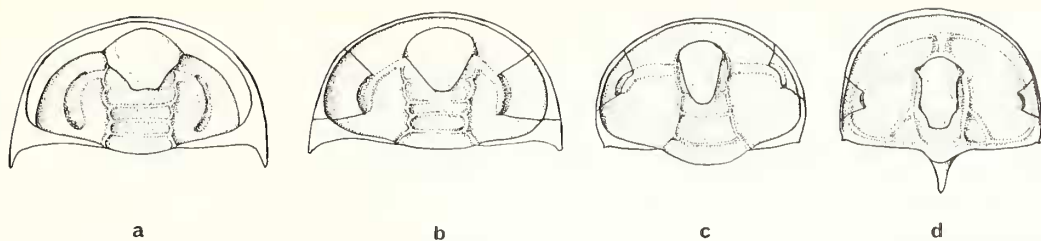
TEXT-FIG. 15. Series of cephalic shields viewed from the ventral side to illustrate why natant condition in Agnostida is not homologous with that in Libristoma, and, left to right, morphological steps in origin of Agnostida. Only *b* is hypothetical. *a*, primitive condition illustrated by typical conterminant olenellid (*Holmia*, see Whittington 1988*a*) showing long crescentic rostral form, confining other cephalic doublure to narrow selvage; *b*, dorsal sutures have appeared, but calcified rostral plate lost; *c*, most primitive kind of pagetiid (well-defined glabellar furrows, glabella extends comparatively far forwards) based on *Sinodiscus* (Zhang *et al.* 1980, pl. 4, figs. 16–21); *d*, *Pagetia* (based on Whittington 1988*a*) illustrating advanced agnostoid morphology triangular 'basal lobes' (possibly extraglabellar) and glabella further short of cranidial margin.

Another character may be cited in the question of agnostid relationships. No protaspis has been described for an olenellid (Palmer 1957), nor yet for a member of the Agnostina. Since meraspides are well known for both it seems likely that this is a consequence of calcification not having 'spread back' far enough in ontogeny in these groups, which again would be interpreted here as a primitive feature. However, given the other specializations of agnostids, lack of protaspis could well be a secondary loss. J. H. Shergold informs me that he has found an eodiscoid protaspis (Zhang 1989; Hu 1971, pl. 7, fig. 23), which would confirm the latter view. Planktic ostracodes, resembling agnostids in size and putative life habits, undergo accelerated development in the egg stage, and of all the ostracodes only one genus, *Manawa*, has a free-living nauplius larva (Swanson 1989). An alternative view might separate Eodiscina and Agnostina as distinct clades, influenced perhaps by the more general 'ptychoparioid' appearance of the former, is shown also on text-fig. 14. This produces a less parsimonious arrangement of the characters I consider important, and is not favoured.

If these characters are interpreted correctly the Agnostida appear above the olenelloids by virtue of their (primitively present) dorsal sutures but below all other trilobites, including Libristoma, because they had not acquired the advanced rostral form. This position does justify their high taxonomic status, and is also consistent with their early stratigraphic appearance in the Lower Cambrian of, for example, China. The loss of calcification of the crescentic rostral plate is one character (and perhaps the most important) defining Agnostida. They are not part of Libristoma.

DIAGNOSIS AND STATUS OF LIBRISTOMA

The Libristoma may be diagnosed as follows: *Trilobites having natant hypostomal condition, or with secondarily conterminant or impendent hypostomal condition.* Rostral plate bounded by connective sutures primitively present, but may be lost by virtue of fusion of the free cheeks, or replaced by median suture.

If Libristoma is a high level monophyletic taxon then it requires taxonomic recognition. A glance at Harrington's (*in* Moore 1959) review of high level trilobite taxonomy quickly shows that the fate of most of the proposed high level taxa in the past has been oblivion. Few authors use such orders as Miomera, Epiparia, Polymera or Protoparia at the moment, and none of these is equivalent to Libristoma. Miomera and Polymera are occasionally employed by Cambrian specialists (Robison 1988); Miomera is equivalent to Agnostida as used here, while Polymera is an unnatural taxon used to encompass the rest of the non-agnostid trilobites. In dealing taxonomically with the new phylogenetic concept implied by Libristoma there were two choices.

1. To redefine the Order Ptychopariida to equate with Libristoma. This would mean that major

monophyletic taxa within the redefined ptychopariids would become suborders. This would include Proetida, which has been regarded as a separate order, although Lütke (1980) regarded Proetida as a ptychopariid suborder. Also, for reasons explained below, the suborder Ptychopariina resulting from this classification would be paraphyletic, and it is perhaps wiser to provide a clear nomenclatorial distinction between an allegedly monophyletic group (libristomates as a whole) and its least satisfactory subgroup.

2. To propose Libristoma as a Subclass. In this case the major groups within Libristoma can be regarded as Orders, which does least violence to the existing classification. This runs the risk that Libristoma, like the major subdivisions proposed in the past, will simply not be used. On the other hand, if it *is* a good monophyletic taxon it should survive by virtue of the light it casts on major phylogenetic events in trilobite history. The trouble with, say, Størmer's (1942) Order Proparia (including eodiscids, norwoodiids, burlingiids and Phacopida on the basis of proparian facial sutures) was not so much the high level status of the taxon involved as the fact that it has subsequently been proved to be a polyphyletic assemblage.

For the moment I prefer the second option. A stricter cladist would insist that a full phylogenetic analysis of the whole group be carried out before the question of taxonomic status is decided. I accept that this kind of study may alter the status of the subgroups within Libristoma. For the moment a pragmatic option is to retain major monophyletic subgroups of Subclass Libristoma as Orders or Suborders, which is what is done below. Suborders are retained within Ptychopariida for no better reason than traditional usage, and this may well change in the future.

Orders and suborders within Libristoma and their diagnoses

The subgroups within Subclass Libristoma should be definable on autapomorphies, with the natant hypostomal condition being the synapomorphy uniting the whole group. A list of primitive characters within the accepted 'Ptychopariida' was given by Fortey and Chatterton (1988, table 2). These include: rostal plate present (transverse width not exceeding that of glabella); tapering glabella with three pairs of glabellar furrows which are shorter anteriorly; a relatively large number of thoracic segments with unspecialized articulation; opisthoparian sutures; terrace ridges on doublure; genal spines present; unspecialized hypostome of the kind discussed above. Most of these characters are present also in redlichiids and are therefore simply characters of all trilobites of the Redlichiid + Libristoma clade: for example, genal spines; opisthoparian sutures; large numbers of thoracic segments; larval hypostomal margin with fringe of spines; glabellar form in many species of redlichiid; terrace ridges on doublure (Kobayashi and Kato 1951, pl. 5, fig. 6; Hupé 1953, pl. 9, fig. 9). With the exception of opisthoparian sutures and the glabellar form, most of these characters are also present in olenellids, and if the olenellids are regarded as trilobites, such characters are simply generalized characters of the trilobites as a whole (Fortey and Whittington 1989). So diagnostic characters of subgroups of Libristoma must comprise characters outside this list.
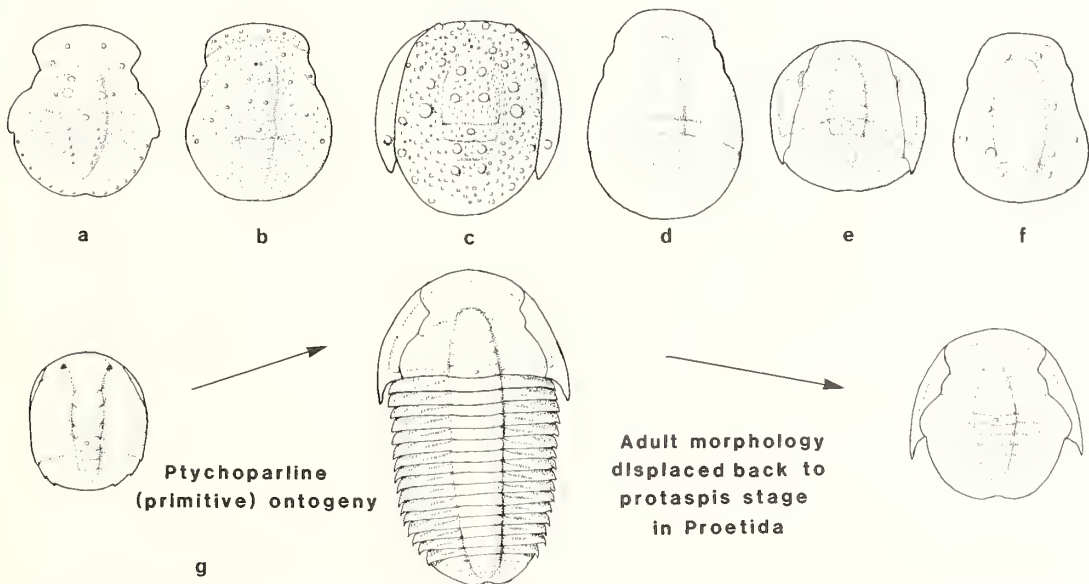
Order PROETIDA Fortey and Owens, 1975

Diagnosis. Libristoma having fusiform glabella in the protaspis stage, and natant hypostomal condition attained early in ontogeny. Larval hypostome margin lacking spines. Most species natant also in adult; some secondarily conterminant or impendent. Median occipital tubercle usually present.

Fortey and Owens (1975) proposed Proetida for what they regarded as a major natural group of trilobites which had been incorrectly classified in the *Treatise* (Moore 1959). Despite the criticisms of Bergström (1977) Proetida has gained wide acceptance since, and some additional taxa have been added to the group (e.g. Telephinidae by Chatterton 1980). Lütke (1980) recognized the group as a suborder of Ptychopariida, and therefore part of the 'ptychopariid problem'. Fortey and Owens' original list of attributes of Proetida was based on what they regarded as overall similarity of the taxa included, without critical assessment of what characters were plesiomorphic and what derived. Part of their argument for monophyly stemmed from a stratigraphical/morphological hypothesis that all Proetida could be derived from the early Ordovician

Hystricurinae. Now that it has been recognized that the majority of Proetida (and all primitive ones) had natant hypostomal condition it is possible to apply a more critical judgement to the characters on which the group is based. If it is a natural group there should be a synapomorphy defining it, whether or not the hypothesis of hystricurine derivation is correct. Many of the proetide characters Fortey and Owens listed (1975, pp. 235–6) are generalized 'ptychopariid' (cf. Fortey and Chatterton 1988, table 2) or even belong to the whole Libristoma: they will not suffice for the definition of the group. Bergström's (1977) criticisms were justified on this point. For example, the hypostomal form described by Fortey and Owens is simply that of the typical natant trilobite (text-fig. 11), while the presence of terrace ridges on the doublure is an even more symplesiomorphic character, being present in Redlichiida and even Olenellida also.

Fortunately for the concept of Proetida there *is* a derived character uniting the group, but this does not become apparent until the hypostomal condition is brought into the argument. Fortey and Owens (1975) did point out that early growth stages of Proetida resembled one another, and illustrated early meraspide cranidia of various families showing tapering, rather elongate glabellas with a deeply parabolic outline. A preglabellar field was present even at this early growth stage. Chatterton (1980) and Fortey and Chatterton (1988) noted the similarity of proetide protaspides. These differ from the typical 'ptychopariid' (text-figs. 9 and 10) in having a fusiform, anteriorly rounded or pointed glabella. That this is general for the Proetida is demonstrated (text-fig. 16) by the occurrence of proetide type protaspides in Proetidae (*Proetus*, see Chatterton 1971, pl. 16, fig. 1), Bathyuridae (*Licnocephala*, see Ross 1953; *Bathyurus*, see Chatterton 1980), Aulacopleuridae (*Harpidella*, see Chatterton 1971, pl. 18, fig. 20; *Scharyia*, see Šnajdr 1981), Dimeropygidae (*Dimeropyge*, see Tripp and Evitt 1983), and Telephinidae (*Phorocephala* (*Carrickia*), see Chatterton 1980; also *Carolinites*, see Fortey 1975, pl. 36, figs. 12–15 meraspides). It is reasonable to assume that the proetide protaspis type was present throughout the group.

a   b   c   d   e   f

Ptychoparline
(primitive) ontogeny

Adult morphology
displaced back to
protaspis stage
in Proetida

g

TEXT-FIG. 16. Late protaspides of various families within Proetida to show synapomorphy of tapering glabella (which falls short of border in these late protaspides); compare text-fig. 10 *h–m*. *a*, *Scharyia* (Scharyiinae; Aulacopleuridae) (after Šnajdr 1980, text-fig. 1*d*), ×20; *b*, *Phorocephala* (Telephinidae) (after Chatterton 1980, fig. 5), ×40; *c*, *Dimeropyge* (Dimeropygidae) (after Tripp and Evitt 1983, pl. 31, figs. 16–21), ×40; *d*, *Bathyurus* (Bathyuridae) (after Chatterton 1980, fig. 5, and pl. 6, fig. 4), ×25; *e*, *Proetus* (Proetidae) (after Chatterton 1971, fig. 15*c* and *d*), ×20; *f*, *Aulacopleura* ? (Aulacopleurinae; Aulacopleuridae) (after Hu 1971, pl. 23, fig. 8; note: Hu assigned the species from which this protaspis is taken to the Proetidae and the genus *Phaseolops*; it seems to the writer far more likely to be an aulacopleurid; also Hu's drawing of the protaspides (his text-fig. 53*a–d*) misinterprets the glabellar shape, and the illustration here is based on the photograph cited). *g*, heterochronic hypothesis for the origin of the proetide type protaspis from the conventional libristomate development (see text-fig. 9).

Because the protoglabella in this kind of protaspis falls somewhat short of the border the proto-hypostome corresponding with the forward part of the glabella must lie a little to the posterior when compared with the ptychoparioid protaspis. At the smallest protaspis stages (at which the rostral plate has not yet developed) Tripp and Evitt (1983) show the proto-hypostome attached to the doublure in *Dimeropyge*, and Chatterton (1971) has indicated that the same applied to the earliest proetid growth stages. Šnajdr's (1981) full ontogeny of *Scharyia* shows that the preglabellar field lengthens during protaspis ontogeny. By the earliest meraspis the cranidial border is clearly developed and Šnajdr's plate 2, fig. 7 also shows that the genal doublure is both coincident with the border, and much narrower (sag.) than the preglabellar field separating the tapering glabella from the border. The hypostomal condition must have been natant. The same argument can be repeated for the meraspis cranidia of the Proetida shown in Fortey and Owens (1975, fig. 3), spanning most of the proetide families. A full ontogeny of hystricurids is not described, but a very small cranidium of *Parahystricurus oculirotundus* Ross (1951, pl. 12, fig. 33) shows identical features, and, because the cephalic doublure is known to be narrow in that species, it is likely that the early onset of the natant hypostomal condition applied also to the hystricurids. It is possible that the natant condition extended even into the protaspis in *Scharyia*, which has a wide area in front of the proto-glabella from the earliest protaspis stage. The spinose margin of the larval hypostome is a character shared by almost all trilobites (Fortey and Whittington 1989), and could be argued to be a synapomorphy of the whole group. But in Proetida for which larval hypostomes have been described (e.g. *Proetus*, see Fortey and Chatterton 1988, fig. 13; *Dimeropyge*, see Tripp and Evitt 1983) the spinose margin is apparently lacking. In this respect these larval hypostomes are more like that of the adult, and differ from immature hypostomes of all other trilobites.

The Proetida can thus be defined within the Libristoma by their protaspis type, and by the 'displacement back' of the natant hypostomal condition, and probably the non-spinose hypostomal margin, into early ontogeny. Because some stratigraphically late Proetida (above) become secondarily conterminant and impendent it is likely that there were reversals (i.e. natant to conterminant) in the ontogeny of such forms, but because they are undisputed proetids this does not pose a problem for the definition of the group as a whole. What is less certain is whether the neat 'cut-off' at the Cambrian-Ordovician boundary suggested by Fortey and Owens (1975) applies with the definition of the Order given here. Fortey and Owens based their stratigraphic definition of the group on the hypothesis that Proetida were all derived from hystricurines. While this is reasonable for dimeropygids and bathyurids (and probably telephinids) for which there are a series of intergrading species between hystricurids and the derived families, this is much less clear for proetids and aulacopleurids. It now seems perfectly possible that one or more Upper Cambrian families will prove to have a proetide protaspis – and if this is the case they, too, should be assigned to Proetida. Solenopleuridae is an obvious candidate; some Cambrian solenopleurids seem to me indistinguishable from Ordovician *Hystricurus*. Ontogenetic studies on trilobites in the later Cambrian, or even the mid Cambrian, might well reveal an extension of Proetida from its present post-Cambrian assemblage of families. Dimeropygidae are better placed in the superfamily Bathyuracea, rather than in Proetacea as in the 1959 *Treatise*.

Order ASAPHIDA Salter, 1864, emend. Fortey and Chatterton, 1988

Diagnosis. Libristoma having ventral median suture. Only primitive forms retain natant hypostomal condition, the majority of the group being conterminant or impendent. Higher Asaphida also have a distinctive inflated protaspis – the asaphoid protaspis.

This major group was defined at length by Fortey and Chatterton (1988) to which paper the reader is referred for details. It was treated as a suborder there, pending further discussion of the ptychopariid problem. If the concept of the Libristoma is accepted its rank can be elevated to Order as discussed previously. Shergold and Sdzuy (1984) have already employed Asaphida as an order, although with a more restricted view of what trilobite groups should be placed within it than that of Fortey and Chatterton (1988). The superfamilies Anomocaracea, Asaphacea (incorporating Ceratopygacea), Remopleuridacea, Dikelocephalacea, and Trinucleacea were included in Asaphida in that work, together with a number of additional families, such as Pterocephaliidae and Dikelokephalinidae. To this list can be added the family Parabolinoididae. Westrop (1986) has recently described a ventral median suture for this group, and because this is the main synapomorphy of Asaphida this is where the family belongs unless it can be shown that the median suture was independently derived therein. Parabolinoididae are interesting in that the bulk of their morphology is almost an inventory of primitive and generalized ptychoparioid characters (Fortey and Chatterton 1988, table 2). As Westrop has pointed out they resemble olenids in many features – but we know that olenids were derived from

ptychoparioids with a rostral plate, not a median suture, and on our analysis of the characters, therefore, such resemblances are because of symplesiomorphies, and misleading.

The placing of Asaphida within the larger group Libristoma is proved by the apparently universal occurrence of the natant hypostomal condition in the primitive members of the group, which are also the stratigraphically earliest. These include the families Anomocaridae, Auritamiidae, Pterocephaliidae, Parabolinoididae, listed above, and probably Liostracinidae (Fortey and Chatterton 1988, p. 879). For the moment these have been retained in a paraphyletic group Anomocaracea – based on the retention of the natant condition in combination with the median suture – but further analysis should ally these families with one or another of the derived monophyletic groups.

Order PTYCHOPARIIDA Swinnerton, 1915

Suborder OLENINA Burmeister, 1843

Diagnosis. Ptychopariida with thin dorsal exoskeleton; free cheeks yoked together as single unit connected by narrow (sag.) doublure (rostral plate present only in the most primitive members of *Olenus*).

Olenids comprise an accepted monophyletic group (Henningsmoen 1957). Most occurred in dysaerobic palaeoenvironments. Probably more than in any other trilobite group many relationships within the olenids have been determined stratigraphically, especially because of the work of Westergård, Henningsmoen and Kaufmann in Scandinavia. This is possible because their record in the Upper Cambrian 'olenidskiffer' is exceptionally continuous. I see no reason to doubt the phylogenies resulting from this work, even though it has to be said that subfamily relationships are not clear. It is a paradox that the very completeness of the olenid phylogenetic history has probably hindered phylogenetic study of other Cambrian groups. The olenid model dictates that if enough collections are made and enough stratigraphy is done the phylogeny will simply 'fall out' from sequence, allowing a direct reconstruction of the historical tree of descent. However the bulk of the olenids occupied a distinct, stable and peculiar environment, certainly dysaerobic and possibly beneath the thermocline (Fortey 1974; Cook and Taylor 1975), which favours the preservation of a continuous phyletic succession of species. This does not apply to the greater part of the shelf record, nor even to deeper environments in which oxygenation was normal.

As Henningsmoen (1957) noted, the morphological excursions taken by olenids in their long Cambro-Ordovician history makes the framing of a diagnosis very difficult. I introduced the fused free cheeks into the diagnosis (Fortey 1974) and this has been subsequently adopted also by Nikolaisen and Henningsmoen (1985). This fusion is true of all olenids for which the material is adequate to see it, other than the earliest species of *Olenus*, which still have the rostral plate. These species of *Olenus* form the sister group of the rest of the Olenidae. Because they include the type species *O. gibbosus* (Wahlenberg) it is obviously necessary to 'draw the line' for the family below these species. An important point is that the fused cheeks of olenids are not homologous with those of Asaphida which develop them (Kainellidae, Nileidae and Cyclopygidae) because they result from the loss of a rostral plate, not a median suture. All olenids except possibly the stratigraphically youngest *Triarthrus* (Whittington and Almond 1987) apparently retain the natant hypostomal condition, but it would not be surprising to find other examples of secondary conterminant hypostomal condition among pelturines with reduced preglabellar fields. In any case (cf. Nikolaisen and Henningsmoen 1985) one cannot incorporate the natant condition into the diagnosis as it is the general character of Libristoma.

There is now the greater problem of whether families other than Olenidae can be assigned to Olenina. Various attempts have been made in this direction. One problem is that unrelated trilobites may have 'olenimorph' features (such as numerous narrow thoracic segments with wide pleurae, long genal spines, caecate dorsal surface) because they, too, became adapted to the dysaerobic environment. Good examples would be *Hedinaspis* among the Asaphacea, *Aulacopleura* among Proetida, *Seleneceme* among Trinucleacea. In the *Treatise* (Poulsen *in* Moore 1959) the family Papyriaspididae was included; as we have noted above there is no evidence to support this, apart from generalized ptychopariid similarity. Palmer (1965) has stated that *Aphelaspis*, which is not a pterocephaliid, might be related to Olenidae. Shergold (1980) included Elviniidae in Olenacea. Westrop (1986) included not only this family, but Idahoiidae, Parabolinoididae, and Ptero-cephaliidae in the same superfamily. In the analysis of Fortey and Chatterton (1988) these last three would be part of Asaphida, having a median suture. The problem is that I can find no synapomorphic characters to link any of these families to Olenidae in particular. The characters they share are all those of primitive ptychopariids. Westrop (1986) states that he followed Ludvigsen and Westrop (1983) in the reasons for associating his selection of families with Olenidae, but in the latter paper there *are* no characters listed that

might unite such a group. One has to conclude that the association is made on 'general' resemblance and on the stratigraphic presumption that they are all similar enough in age to be likely to constitute a natural group. Obviously Olenidae had to have a sister group, and I am certain that a major libristomate group including the olenids will be recognizable. At the moment I can see no characters to define such a group. For this reason Olenina are retained as a suborder of Ptychopariida *faux de mieux*. I think it wiser to restrict the scope of Olenina to a genuinely monophyletic group, rather than cram in other families on spurious grounds with the risk of creating a polyphyletic taxon.

Suborder HARPINA Whittington, 1959

Diagnosis. Libristoma having small eyes placed anteriorly relative to glabella; cephalon broadly convex (sag. tr.) with long preglabellar area, and often a brim, with stout genal spines or genal prolongations of the brim; free cheeks narrow (tr.) or lost altogether, fused together; thoracic segments numerous (12 or more) and characteristically narrow (sag.) with long pleurae in contact along their length; pygidium relatively small and often transverse.

The natant condition of the hypostome of *Harpides* is clearly illustrated on the holotype of the type species illustrated by Barrande (1872), and was suggested for Harpetidae by Whittington (1988*b*, p. 328); I know of no harpinid in which the hypostome has become secondarily conterminant. Even the earliest harpidinids (which are found at an horizon close to the Cambrian-Ordovician boundary) are specialized in most respects. There is no better hypothesis available for their Cambrian ancestry than that they are related to the Upper Cambrian to early Ordovician genera *Loganopeltis* and *Loganopeltoides*. *Loganopeltoides* still has narrow free cheeks, defined by sutures which are subparallel and close (Rasetti 1945). Rasetti (1948) demonstrated how a harpid-like cephalon could result from 'closure' of these sutures leaving the eyes isolated within the genal fields, a situation seen in the *Harpides*-like genus *Loganopeltis*.

All Harpina have the doublure fused as a single piece, as do loganopeltids and entomaspids (Rasetti 1952*b*; Ludvigsen 1982) which were placed in Harpina in Moore (1959). However, if the Harpina belong within the Libristoma the ancestor from which the group derived presumably carried a rostral plate, which was lost in the same fashion as in Olenina. At some stage also there must have been a change from a normal opisthoparian facial sutures. Ludvigsen (1982) assigned the genera *Heterocaryon* and *Bowmania* to Entomaspididae, both of which have normal opisthoparian sutures. He also placed the Entomaspididae in the superfamily Solenopleuracea, and hence presumably regarded them as unrelated to Harpina. If this were the case then presumably the harpinid features of entomaspids would have to be evolved in parallel, which would be hard to prove because Solenopleuracea has no autapomorphies. Ludvigsen also drew attention to the resemblance between entomaspids and the older genus *Doremataspis* Öpik, 1967 – which Öpik placed in another superfamily, Liostracinacea. This is some measure of the confusion pertaining in Cambrian trilobite classification. It is worth mentioning that there are some similarities also between Harpina and the mostly Upper Cambrian Superfamily Norwoodiacea: anterior position of small eyes, stout genal prolongations, wide and flat thoracic pleurae, and a tendency for the reduction of free cheeks (*Norwoodia* has strongly proparian sutures which have become almost parallel in the fashion of *Loganopeltoides*). Again, homoplasy will no doubt be invoked to explain these similarities. The best that can be said is that the Harpina have no recognized sister group, and to follow existing usage in retaining it as a suborder of Ptychopariida.

Suborder PTYCHOPARIINA Swinnerton, 1915

Diagnosis. A paraphyletic libristomate group retaining primitive characters; a combination of: relatively narrow rostral plate present, glabella barrel-shaped to tapering; natant hypostomal condition (possibly some secondarily conterminant); hypostome unspecialized; protaspis with forward-expanding axis reaching far forwards; with few exceptions micro- to heteropygous.

It is now possible to return to the 'ptychopariid problem' in the context of the recognition of the monophyletic groups listed previously. Having 'hived off' these natural groups there remain a collection of families which do not have the derived characters typifying these groups (or in which such characters are not known because of the poor state of knowledge of the ventral sutures and/or ontogeny of the group). What characters there are are often those of *Ptychoparia* itself, and primitive for Libristoma as a whole. Because we *cannot* yet assign such trilobites as more closely related to one or another of the derived groups there is little choice but to retain

a Suborder Ptychopariina for their reception. Because they include the primitive libristomates they are considered here to have descended from a common ancestor; because they also will include the sister taxa of Proetida, Olenina, Asaphida, and presumably Harpina, the Ptychopariina constitutes a paraphyletic assemblage. Ptychopariina can only be defined as being libristomate, but not having one or another of the synapomorphies that define the monophyletic Orders or Suborders. This is scarcely satisfactory, and to a strict cladist not acceptable at all. I would regard it only as a convention to accommodate primitive libristomates until they can be related to one or another of the derived groups. Before this can be done, I believe more characters will have to be brought into play than I have considered in this paper.

Such a concept of the Suborder Ptychopariina would result in the inclusion of the following superfamilies (uncritically culled from Moore 1959): at least some Ellipsocephalacea (transferred from Redlichiida, see above); Ptychopariacea; Conocoryphacea; Crepicephalacea; Illaenuracea; Solenopleuracea; Asaphiscacea; Komaspidacea (excluding Telephinidae which are Proetida); Raymondinacea; Norwoodiacea (unless they prove to belong in the Harpina); and Marjumiacea. Some groups included in Ptychopariida in the *Treatise* (Moore 1959) would be excluded because they were probably not natant, especially Leiostegiacea and Damesellacea. I return to these below.

One can be critical of almost all the superfamilies of Ptychopariina as natural groups, and this has been reflected in a reluctance to employ these higher categories by more cautious authors such as Robison (1971) and Zhang and Jell (1987). The whole group needs proper phylogenetic analysis. It can be noted that:

1. Conocoryphacea is almost certainly polyphyletic (contrast Eldredge 1977). The uniting character is loss of eyes. This character is known to be derived many times in the history of the trilobites, for example, in Proetida, Phacopida, Trinucleacea and Agnostina. A comparison of the contrasting glabellar structures of such conocoryphacean genera as *Bailiella*, *Conocoryphe*, *Hospes*, *Hartshillia* and *Shumardia*, shows that they are more likely to be more closely related to disparate (but eye-bearing) ptychopariids than to one another. For example, *Bailiaspis* might be related to *Solenopleura*, *Conocoryphe* to *Ptychoparia*, on the basis of their cephalic morphology. The conocoryphaceans do not even 'lose' the eyes in the same way: *Bailiella* has short, 'marooned' eye ridges and comparatively wide fixed cheeks, while *Conocoryphe* and *Meneviella* have long genal ridges and marginal sutures. The Conocoryphacea has simply been used as a taxon to collect together blind ptychopariids which are merely the result of (especially Middle Cambrian) adaptations to off- or outer-shelf atheloptic situations.

2. It is scarcely possible to produce a differential diagnosis of Ptychopariacea, Solenopleuracea and Marjumiacea which presumably should be possible if any one of them is a natural group. As it is, they encompass only primitive ptychoparioid morphologies.

3. Illaenuracea and Raymondinacea are strikingly heterogeneous groups, which are not definable; some of the families within these groups have already been reassigned (e.g. by Westrop 1986), and the coherence of those remaining is in doubt.

4. Komaspidacea and Norwoodiacea are probably natural groups, but as with the Olenina their sister group relationships are uncertain.

These problems are enough to show that we have no idea at present on how to dismantle the Ptychopariina as a paraphyletic group, even with the restriction on the definition of the group I have introduced in this paper. Further stratigraphical studies may allow for the recognition of monophyletic subgroups, but if the lack of success in the past is any guide, it seems most unlikely that stratigraphic series will do more than resolve a few generic relationships, leaving the broader issues untouched. The future seems to me to lie in the recognition of monophyletic groups, and the recognition of their sister groups within the Ptychopariina, which will allow those groups to be 'hived off' into the derived group (similar to the way in which Fortey and Chatterton (1988) placed the 'ptychoparioid' anomocaraceans into the Asaphida). Even so there will probably remain a core of ptychopariids sharing only the primitive grade of libristomate organisation, and differing only in characters of the most trivial kind (see, for example, the ptychopariid subfamily Antagminae, Rasetti *in* Moore 1959, p. 236). These will likely remain classified together, as perhaps they should.

## CLASSIFICATION OF TRILOBITE GROUPS FORMERLY REGARDED AS PTYCHOPARIIDS

If it is correct to regard the Libristoma as a monophyletic group, trilobites which do not have natant hypostomal condition (or did not have a natant ancestor) are classified elsewhere. They are not part of the 'ptychopariid problem' except insofar as they have been classified with Ptychopariida in the past. This applies to the following superfamilies in the 1959 *Treatise*: Damesellacea, Leiostegiacea

(including Tsinaniidae), Illaenacea (which excludes proetids and relatives) and Calymenacea by virtue of their supposed ptychopariid origins. The important question about non-natant groups where their ancestry is uncertain is whether they were primitively conterminant or whether they were secondarily so, having been derived from a natant ancestor in the manner of most Asaphina. Unless there is evidence to the contrary it is reasonable to assume that they were primarily conterminant, this being, of course, the primitive condition. This assumption may not prove to be justified, especially with regard to the Phacopida.

The superfamilies removed from Ptychopariida (*sensu* 1959 *Treatise*) can be accommodated within other non-libristome groups, as follows. Detailed evidence will be reviewed elsewhere.

1. *Superfamily Illaenacea*. The families Illaenidae, Styginidae (= Scutelluidae) and Phillipsinellidae belong in a monophyletic group termed the suborder Scutelluina (emend. from Superfamily Scutelloidea Hupé, 1953) by Lane and Thomas (1983), for which I retain the older name Illaenacea. This may be part of a larger group to be included within the Order Corynexochida, as noted by Přibyl and Vaněk (1971). Corynexochida is usually considered to be Cambrian, and inclusion of Illaenacea would extend its stratigraphical scope to the Devonian.

2. *Superfamily Leiostegiacea*. With the inclusion of *Annamitella* in the Leiostegiacea (Fortey and Shergold 1984) the range of this superfamily extends from the Cambrian until well into the Middle Ordovician. Few articulated leiostegiaceans are known and our knowledge of the ventral surface is accordingly limited; articulated material of *Leiostegium* was described by Jell (1985), who concluded that a rostral plate was present. The likely conterminant hypostomal condition of leiostegiaceans is shown by the sharp termination of the glabella at the border, at which there are prominent pits to articulate with the anterior wings of the hypostome (text-fig. 17), and by the fact that where the anterior cephalic border becomes wider, as it does in *Palocorona* Shergold, 1975, backward-curving paradoublural lines are developed comparable with those on *Proceratopyge* (see Jago 1987) which are associated with increase in width of doublure medially in conterminant condition. Hence there is no evidence that Leiostegiacea belong to Ptychopariida (or Libristoma).
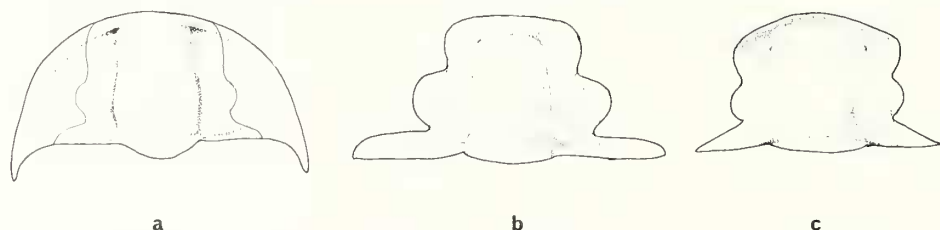
TEXT-FIG. 17. Leiostegiacea and possible relatives. *a*, cranidium of *Leiostegium*, early Ordovician, showing prominent anterior pits at border suggesting conterminant hypostomal attachment, × 3; *b*, cranidium of late Cambrian *Peichiashania* (after Shergold 1980, pl. 27, fig. 1), × 2·5; *c*, early Ordovician *Theamataspis* (Scutelluidae) (after Fortey 1980), × 5. If preoccipital muscle impressions in *b* and *c* are homologous, this may provide evidence of leiostegiacean ancestry of Illaenacea via tsinaniids (see text).

It seems possible that the Leiostegiacea also belongs within the Corynexochid/Illaenacean group. Many leiostegiaceans show a corynexochoid glabellar form: *Leiostegium* (Jell 1985, pl. 22, fig. 11; Shergold 1975, pl. 45, fig. 7), *Pagodia* (*Oreadella*) (Shergold 1975, pl. 36, fig. 1) *Annamitella* (Fortey and Shergold 1984, pl. 34, figs. 1–5, 7) and *Parakoldinioidia* (see Taylor and Halley 1974) from various families. The last-named is a member of the family Missisquoiidae, which was assigned to the Leiostegiacea by Shergold (1980), but which has been claimed (Ludvigsen 1982) as lying at the 'root' of the post-Cambrian radiation of the styginids (a contrary view was expressed by Lane and Thomas 1983). Shergold (1975) assigned the effaced family Tsinaniidae to the Leiostegiacea; in the *Treatise* (Lochman-Balk *in* Moore 1959) this family was considered to belong to Asaphacea (and

hence to Libristoma). I think Shergold is correct in removing tsinaniids from Asaphacea. For all their general dorsal effacement, tsinaniids show prominent muscle impressions lying outside the axial furrow opposite the posterior part of the palpebral lobes. These are like the 'lunettes' of illaenids, and the homologous impression on styginids, and may be a synapomorphy. A similar impression exists on some more conventional leiostegiaceans, such as *Peichiashania* (Shergold 1980, pl. 27, fig. 1; see text-fig. 17 herein). These structures are distinctive enough to suggest they may be homologues. All the evidence combines to indicate that leiostegiaceans may be part of an enlarged illaenid/styginid/corynexochoid group.

3. *Superfamily Damesellacea*. The damesellaceans are regarded as the primitive sister group of the Odontopleurida, and should be placed in that Order. As in that group the hypostomal condition (see, for example, Chatterton and Perry 1983) was conterminant, and there is no evidence to suggest natant ancestry. Characters shared between odontopleurids and damesellaceans include: 1, narrow, (sag.) ledge-like anterior cranidial border, which the glabella abuts sharply; 2, deeply scribed and inflated eye ridges; 3, transverse hypostome with relatively wide posterior border; 4, spinosity, especially pygidium and anterolateral margins of free cheeks (not the odontopleurid *Selenopeltis*); 5, occipital tubercle without thoracic homologues (where known, apparently of Fortey and Clarkson's 1976 type D); 6, third glabellar lobe reduced or absent. The autapomorphy of Odontopleuridae is the unique bi-spinose thoracic pleural tip, not present on Damesellacea (*fide* Lu *et al*. 1965, pl. 72, fig. 6). The apparent stratigraphic gap between Damesellacea (mid to late Cambrian) and Odontopleuridae (early Ordovician to Devonian) has now been bridged with the recognition by Bruton (1983) and Thomas and Holloway (1988) of *Acidaspides praecurrens* Lermontova, 1951, from the Upper Cambrian of Kazakhstan, as a true odontopleurid; the pygidium of this species (Thomas and Holloway 1988, pl. 16, fig. 352) shows more axial segments than Ordovician odontopleurids, but is identical to certain damesellaceans in this regard. Thomas and Holloway (1988) joined many previous authors since Swinnerton (1915) in regarding Odontopleurida and Lichida as together constituting a monophyletic group (as repeated on text-fig. 19). This is not the only possibility, because as many characters support the Styginidae as the sister group of Lichida. Further investigation of damesellids should cast light on this matter.

THE PROBLEM OF THE ORDER PHACOPIDA

The Order Phacopida Salter, 1864 is the largest group outside Libristoma, and may eventually prove to belong within it. In current usage it comprises the Suborders Cheirurina, Calymenina and Phacopina. The Cheirurina and Phacopina are accepted as monophyletic groups, and the Calymenina usually so, but there is no consensus about their mutual relationships. Both Henningsmoen (*in* Moore 1959) and Bergström (1973) indicated 'ptychopariid' origins for Phacopida. The diagnosis of Phacopida by Henningsmoen (*in* Moore 1959) includes no characters peculiar to the group. Eldredge (1977, fig. 8) claimed that Calymenina were unrelated to Phacopina and Cheirurina, and placed them instead as the sister group of 'some Ptychopariina'. This certainly brings the Calymenina within the remit of the 'ptychopariid problem'. The alliance of Calymenina with Phacopida and Cheirurina was based on the close resemblance between their protaspides (Whittington and Evitt *in* Whittington 1954; Whittington *in* Moore, 1959; Chatterton 1971), including the presence of three pairs of prominent marginal spines, of which only two are cephalic (the 'phacopoid protaspis'). Bergström (1973) placed all three suborders (demoted to superfamilies) in different orders: Odontopleurida (Cheiruracea), Phacopida (Phacopacea) and Ptychopariida (Calymenacea). Again, this shows how different are opinions about high level trilobite classification. But whatever classification is closest to the truth, Phacopida have to be discussed in relation to Libristoma.

   A list of possible synapomorphies can be cited as supporting the concept of Phacopida used in the *Treatise* (Henningsmoen *in* Moore 1959), shared between Calymenina, Cheirurina and Phacopina. These are:

1. The phacopoid protaspis type.

2. Loss of concentric terrace ridges on the cephalic doublure. As discussed above, cephalic doublural terrace ridges are primitive for the Trilobita and retained in Libristoma; their loss is significant.

3. Presence of hypostomal wing process. Although not widely figured this has been shown on representatives of all three groups by Whittington (1988*b*), and on an early cybeline by Fortey (1980).

4. Granulose surface sculpture. A characteristic densely granulose surface sculpture appears to be ubiquitous on early representatives of all three major groups (later Phacopina have much modified sculpture, but all stratigraphic evidence shows this to be secondary).

5. Absence of pygidial border in more primitive members of the group. Pleural and interpleural furrows usually extend very close to the margin and do not stop at a marginal upturned pygidial rim or flattened border so common in Libristoma. A 'pseudoborder' may appear on certain homalonotids such as *Plaesiacomia* (Henry 1980, pl. 23, fig. 4), but this is connected with co-aptation, and is not homologous with borders of other trilobites.

6. Five or more pygidial segments. This number is known to be secondarily reduced in later Cheiruridae.

This list is sufficient to suggest that the *Treatise* (Moore 1959) Phacopida *does* constitute a natural group. I cannot find any of the alternative suggestions which have been made regarding ordinal relationships of Calymenina and Cheirurina supported by more characters which are likely to be synapomorphies. For example, of Bergström's (1973, p. 41) list of odontopleurid characters there are only two (nature of thoracic articulation and loss of cephalic doublure terrace ridges) which would support the inclusion of Cheiruracea in Odontopleurida.

If Phacopida includes Calymenina, Cheirurina, and Phacopina it is likely that the suborder Calymenina is the primitive sister group of Cheirurina + Phacopina, as shown by the distribution of characters summarized in text-fig. 18. Detailed discussion of these characters is beyond the scope of this paper, except to note that calymenaceans retain several primitive characters, such as the circum-ocular suture (uniquely among post-Cambrian trilobites) and tapering glabella. The question is whether any calymenines show evidence of having an ancestor with natant hypostomal condition, which would imply that they, like the Asaphida, should be included within Libristoma. All Phacopina and Cheirurina have attached, conterminant hypostomes, and we would expect natant ancestry to be revealed in the most primitive calymenaceans. *Neseuretus* is close to the common ancestor of Calymenidae and Homalonotidae, and, as noted above (text-fig. 3*a*), was conterminant. Probably still more primitive calymenaceans have clear preglabellar fields, and include *Prionocheilus* Rouault, 1847 (= *Pharostoma* of authors) and *Bavarilla* Barrande, 1868. Whittard (1960, pl. 18, fig. 4) illustrated a posterior extension of the doublure/rostral plate in *Prionocheilus* (after the manner of text-fig. 6), and in this form the hypostome was conterminant. So all Phacopida from the early Arenig onwards apparently have attached hypostomes, and the likelihood is that the relevant trilobites will be found in rocks of Tremadoc age or older. *Bavarilla* is Tremadocian, and was discussed in detail by Sdzuy, 1955. Most of its characters are primitive ones, even for libristomates: its hypostome is like that of generalized libristomates (Sdzuy 1955, pl. 6, fig. 50); it retains a pygidial border; it has a pygidium with only two (three?) segments; it does not show basal ('alar') muscle impressions in the cephalic axial furrows. In fact, its only likely phacopide character is the epifacetal type of pleural furrow (Sdzuy, pl. 6, fig. 55). Given that it also had narrow genal doublure (Sdzuy, pl. 6, fig. 52) and a preglabellar field it is not unreasonable to infer that the hypostomal condition was natant, unless the rostral plate were extended in the manner of *Prionocheilus*. So the position of *Bavarilla* as sister taxon of the Phacopida relies on a single character – and stratigraphialc position, which may mislead. Since its hypostome is not known *in situ* its natant character is inferred, and on this alone would reside the placing of the Phacopida within the Subclass Libristoma.

I would be more enthusiastic about including Phacopida in Libristoma if some trilobites existed which had more of the phacopide synapomorphies whilst retaining the natant hypostomal condition. There are some late Cambrian trilobites which show other similarities to Calymenidae.
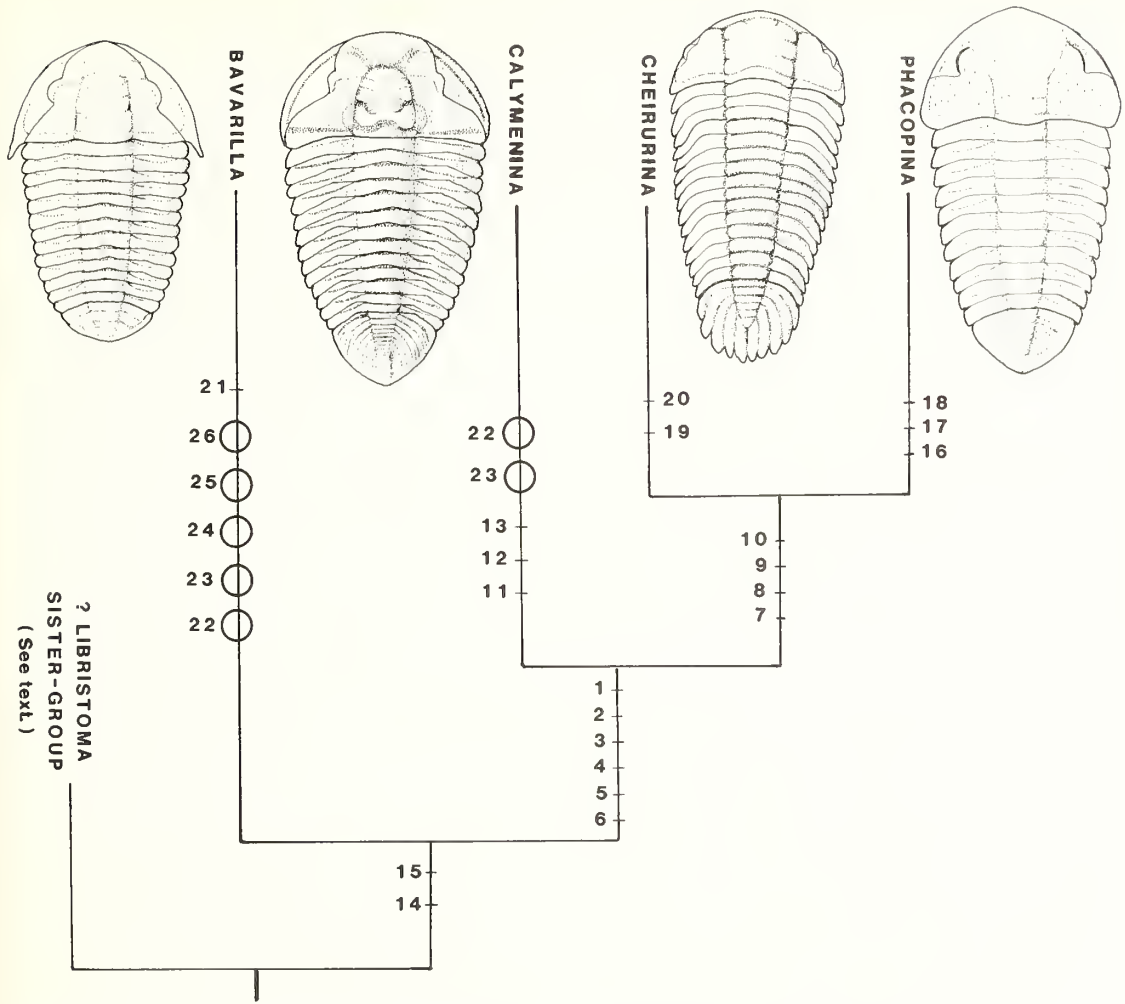
TEXT-FIG. 18. The most parsimonious cladogram of relationships of the main subgroups of Phacopina, emphasizing synapomorphies regarded as important, with *Bavarilla* as the sister group of higher Phacopida; retained plesiomorphic characters are shown as circles. Whether or not this group is a member of Libristoma depends on whether the sister taxon was natant (see text, p. 566). Primitive members of each group are illustrated: Calymenina, *Neseuretus*; Cheirurina, *Pliomerops*; Phacopina, *Ormathops*. Characters: 1, phacopoid protaspis type (protaspis of *Bavarilla* is unknown and may prove of this type); 2, loss of concentric terrace ridges on cephalic doublure; 3, presence of hypostomal wing process; 4, densely granulose surface sculpture; 5, loss of pygidial border; 6, five or more pygidial segments (this character undergoes reversal in later Cheiruracea); 7, proparian suture; 8, forward-expanding glabella (there are a very few exceptions to this in Cheirurina + Phacopina); 9, loss of circum-ocular facial suture; 10, spongy-reticulate genal prosopon; 11, gonatoparian style sutures; 12, muscle pad in 'alar' position; 13, muscle pad at inner end of S1 (which may otherwise bifurcate); 14, loss of falcate pleural tips; 15, epifacetal pleural furrow; 16, schizochroal eye; 17, characteristic sigmoidal form of 3S; 18, loss of rostral plate by fusion of free cheeks (except the primitive phacopide *Gyrometopus* Jaanusson, 1975, which retains it); 19, spinose pygidial margin; 20, cheiruroid type of thoracic articulation (see Bergström 1973); 21, only two deep pygidial pleural, no interpleural furrows. Retained primitive characters: 22, circumocular sutures; 23, tapering glabella; 24, opisthoparian sutures; 25, generalized ptychoparioid glabellar furrows; 26, strong pygidial border.

Calymenidius Rasetti, 1944 has granulose surface sculpture, and similar glabellar structure to calymenids. There are no 'alar' muscle impressions on Cambrian *Calymenidius* spp., although they were present on an early middle Ordovician species described as aff. *Calymenidius* sp. ind. by Whittington (1965, pl. 59, figs. 10, 12–15), a species which might now be referred to *Protocalymene* Ross, a calymenid. *Cliffia* (see also *Kirengina* Ogienko, 1974) is worth mentioning because its pygidium (e.g. Westrop 1986, pl. 27, figs. 4, 6) is at least superficially like those of early calymenids and Phacopina, and the cranidium can be compared with that of *Neseuretus* in the anterior position of the eye, glabellar shape, and the like. It does not show any distinctive cephalic autapomorphy of Calymenina, and nothing is known of the hypostomal attachment. Search for Cambrian sister taxa of Phacopida may not be fruitless. In the meantime the evidence of *Bavarilla* and lonchocephalids such as *Calymenidius* is hardly enough to place Phacopida within Libristoma, to which it might well belong.

HISTORY OF HYPOSTOME ATTACHMENT

The history of hypostome attachment among the non-olenellid trilobites can now be summarized (text-fig. 19). It seems likely to be of considerable importance in understanding aspects of feeding and functional morphology bearing on the adaptive history of the group as a whole. Early Cambrian redlichiids had conterminant hypostomes. On other early Cambrian trilobites, like *Dolerolenus*, the preglabellar field became extended, the cranidial border was extended backwards as a plectrum, but the hypostome may have become detached from the doublure at later stages in the ontogeny. Redlichiid conterminant condition was retained and modified in paradoxidids, in which both the frontal lobe of the glabella, and the middle body of the hypostome became inflated. Spinose projections on the posterior margin of the hypostome, such as those on paradoxidids, are a common feature of trilobites with attached hypostomes throughout the Palaeozoic. If it is correct to identify the ancestry of corynexochid-styginid-illaenid and the odontopleurid-lichid groups within what would be currently classified as Redlichiida these groups originated in the Lower Cambrian and retained the primitive conterminant mode of hypostomal attachment until the very end of their history in the Devonian. By the mid Cambrian corynexochids included superficially asaphid-like trilobites (*Glossopleura*), and others that resembled Ordovician or later styginids, but in all of these rostral plate and hypostome were fused together.

The first Libristoma also appeared in the Lower Cambrian among the protolenids, trilobites which otherwise resemble contemporary redlichiids closely. The major 'radiation' of libristomates was in the middle part of the Cambrian, when highly effaced forms, or genera with eyes reduced or lost (polyphyletically), are found in different palaeoenvironments, sometimes to the exclusion of other trilobites. These libristomates may have been the first trilobites to exploit particle-feeding in deep sea environments. Libristomate hypostomes remained unspecialized for much of the Palaeozoic. One kind of conservative libristomate morphology persisted with little change from *Elrathia*-like forms in the mid Cambrian to *Aulacopleura*-like forms in the Devonian. Before the end of the Middle Cambrian the ventral median suture had developed in 'anomocaracean' asaphide libristomates, and the earliest secondarily conterminant hypostomal attachment appears in the asaphide group (*Proceratopyge*) shortly afterwards. In the Upper Cambrian these secondarily conterminant forms became important components of shelf faunas (Dikelokephalacea) but many different kinds of libristomates with unattached hypostomes persisted, notably Olenidae, which successfully occupied dysaerobic environments. Secondarily conterminant Asaphida started to develop modifications of the hypostome, such as wide borders, and posterior forks. It is interesting that the diversification of secondarily conterminant forms followed the eclipse of the primarily conterminant Corynexochida, some of whose morphologies they broadly reproduced. The Upper Cambrian record is overwhelmingly dominated by Libristoma, but if the relationships suggested in this paper are correct, primarily conterminant forms related to the lichid-odontopleurid and styginid-illaenid groups persisted through this interval. The Leiostegiacea and Damesellacea are regarded as primarily conterminant groups that bridge this 'gap'.
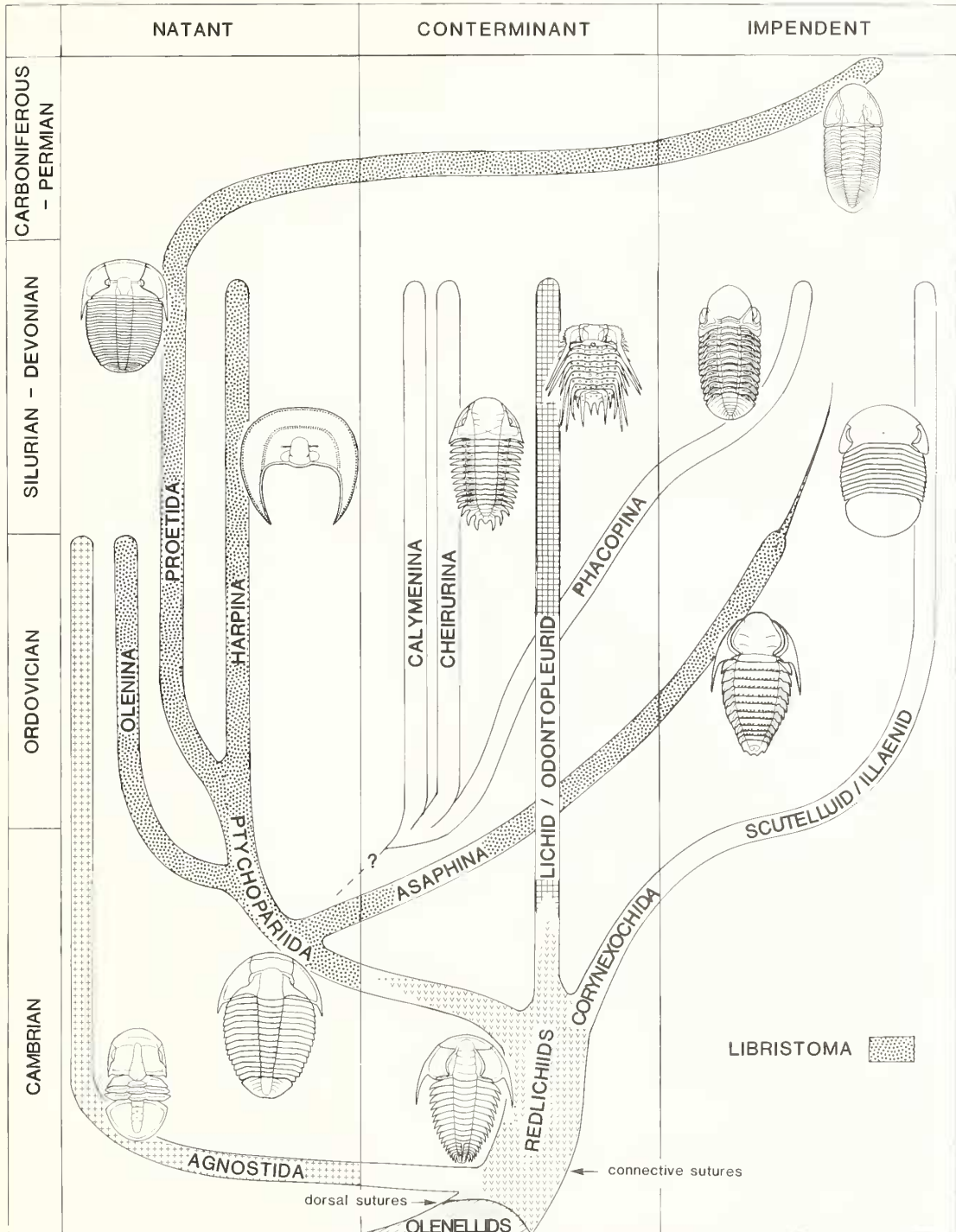
TEXT-FIG. 19. Simplified summary of history of hypostome attachment and the phylogeny of Trilobita, drawn as a tree. Secondary conterminant and impendent forms are derived from proetide sources after the disappearance of other conterminant clades. This may have happened first in the Silurian, but is not shown here for reasons of clarity.

By the early Ordovician natant hypostomes were confined to Proetida, and to a number of specialized groups persisting from the Cambrian (Trinucleacea, Harpina, Agnostina and Olenidae). Secondarily conterminant asaphids and remopleurids were important and characteristic components of Ordovician faunas, but did not survive the Ordovician-Silurian boundary, at which level most of those natant families persisting from the Cambrian also became extinct (trinucleids, agnostids, olenids). At the same time the secondarily conterminant Asaphida also died out. Phacopida were important from the Ordovician onwards; all those we know had attached hypostomes, but the question of whether they had a natant, or primary conterminant ancestor is not satisfactorily resolved (see p. 565). The Odontopleuridae, Lichidae, Styginidae and Illaenidae with primary conterminant hypostomes diversified in the Ordovician and passed through to the Silurian and Devonian. Impendent hypostomal condition was common in the Ordovician (Cylopygacea, Illaenina, later remopleuridids) for the first time. Those groups with attached hypostomes developed hypostomal specializations in the Ordovician: forks, wide borders, enlarged maculae, varied surface sculpture. Natant hypostomes remained similar to those of the Cambrian.

From the Silurian onwards the natant condition persisted in Proetida alone, but within this group certain forms (*Warburgella, Cordania*) became secondarily conterminant. Again, one might speculate that these forms were filling niches unoccupied since the extinction of conterminant asaphides. In the Silurian impendent phacopids became widespread, and these continued into the Devonian.

After the end-Frasnian extinction of major trilobite groups, Proetida alone survived. Some of these were natant. But secondarily conterminant genera, such as *Paladin*, are also common trilobites in the Carboniferous – these developed hypostomal specializations like those of other conterminant trilobites. Certain phillipsiids (*Paraphillipsia, Cyphinioides*) became impendent, the first proetides to be so. I suspect that only secondarily conterminant and impendent hypostomal attachment persisted into the Permian, and the end of trilobite history (Owens 1983 has illustrated the relevant genera, none of which has a preglabellar field). So by the Carboniferous one group of Proetida were exhibiting the whole range of hypostomal attachment modes, although this group as a whole was primitively, and persistently, natant. As has been recognized for some time, some of these Carboniferous trilobites show parallelisms to earlier and unrelated groups – such as Phacopida. It does not seem likely to be coincidence that the proetids show such morphological novelty only after the demise of the conterminant groups (or impendent groups derived therefrom) which may have persisted all the way from the Lower Cambrian.

REMAINING PROBLEMS

Further problems in trilobite classification are legion. A number arise out of my analysis.

1. The relationships between the major subgroups of Libristoma, here treated as Orders and Suborders, are not resolved.

2. The relationships between the other high level taxa having primary conterminant hypostomal attachment are not resolved, neither between themselves, nor with the Libristoma. These appear merely as 'other trilobites' on text-fig. 14. These comprise, at the least: the Corynexochid/Illaenid/Leiostegiacean group; the Lichid/Odontopleurid group (if it is one); the Phacopida. Such evidence as there is, and it is feeble, places the last-named within Libristoma.

3. Redlichiida is only defined by not having one of the advanced characters of the other major trilobite groups with a rostral plate bounded by connective sutures. It is certainly a primitive group, and probably a paraphyletic group, which requires further analysis. Stability on the taxonomic status of higher level taxa cannot be achieved without resolution of some of these problems.

4. All these problems would benefit from phylogenetic analysis using one of the parsimony-based computer programmes for the production of dichotomous trees. The change from natant to secondarily conterminant is a major character reversal according to my treatment, and it would be interesting to see whether this was supported by other methods of analysis.

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